BREEDING OF THE GREY WARBLER WITH SPECIAL REFERENCE TO BROOD-PARASITISM BY THE SHINING CUCKOO

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CONTENTS

ABSTRACT

Between 1976 and 1979 I sought to document and understand territoriality and breeding in the grey warbler (Gerygone igata), and brood-parasitism of the warbler by the shining cuckoo (Chrysococcyx lucidus), at a kanuka-forest near Kaikoura (South Island, New Zealand).

Grey warblers held territories of about 0.7 ha. The average annual mortality of breeding-birds was only 20%, and the predicted average life-expectancy of adults five years. The warbler's breeding-strategy was unusual: the breeding-cycle was protracted; eggs of a clutch were laid 48 hours apart; each egg was 23% of the mean adult weight; nestlings apparently gained weight according to a truncated normal curve, and they exceeded adult weight by up to 40%. This strategy may be an evolutionary response to a relative scarcity of food during breeding.

Each parasitised nest received one cuckoo-egg, apparently swapped for a host's egg. Shining cuckoos lacked egg-mimicry. The cuckoo's egg was similar in size to the warbler's, but was heavier relative to adult weight than in other cuckoos. Cuckoos laid during 10 weeks, the modal week of laying following the apparent peak of arrival of cuckoos in New Zealand by seven weeks. Cuckoos often laid after warblers began incubating. Nestling cuckoos evicted all other nest-contents at 3-7 days old.

Parasitism reduced by only 17% the production of fledgling warblers from late nests. Cuckoos had little effect on the warbler's overall reproductive success because no first nests and only 55% of late nests were parasitised. The mean weight of nestling cuckoos never reached that of a brood of four warblers of comparable age. On average a cuckoo was brooded more than broods of warblers, but was visited with food less often than the host's own young in broods of three or four.

1. INTRODUCTION

Breeding of the passerines and cuckoos native to New Zealand is little known partly because the country is sparsely populated, and ornithologists are few in relation to the tasks at hand. There is also an over-riding physical constraint: most native passerines are restricted to native forest comprising tall evergreen trees in which close observation and the finding of nests is difficult.

The grey warbler (Gerygone igata Muscicapidae: Malurinae) is one of the few native passerines that persists in habitats modified by man. It is common throughout mainland New Zealand and on most off-shore islands, from the Three Kings Islands to Stewart Island and its outliers (Oliver 1955, Bull et al. 1978). Grey warblers occasionally visit the Snares Islands (105 km SW of the southern tip of Stewart Island), although they have not established (Horning and Horning 1974). Grey warblers occur from sea-level to 1400-1500 m (Sibson 1958) in most types of native forest, apparently with a preference for indigenous and exotic scrub. They occur in many other situations, from coastal sand-dunes, swamps, mangroves and river-beds to the sub-alpine zone, and they also breed in pine-plantations, farmland, parks and gardens. The sexes of grey warbler are superficially alike. Grey warblers and riflemen (Acanthisitta chloris) weigh 6-7 g and are the lightest New Zealand birds.

The grey warbler's brood-parasite, the shining cuckoo (Chrysococcyx lucidus lucidus Cuculidae: Cuculinae), is as widespread during its months in New Zealand as its host (Bull et al. 1978). Sagar (1977) reported a shining cuckoo on the Snares Islands, and Oliver (1955) listed the species from the Kermadec and Chatham Islands. The cuckoo occurs in all vegetated and cultivated habitats to about 1200 m a.s.l. (Falla et al. 1970). Stidolph's study (1939) of the grey warbler and shining cuckoo in the Wairarapa lacked a numerical base.

The objectives of this study were to document the breeding of grey warblers and shining cuckoos, and the parasitic interaction linking the two species. Four aspects were considered.

(1) Timing. When do warblers and cuckoos breed and how are the various stages of the two breeding-cycles organised and timed both independently and in relation to the other?

(2) Numbers. What proportion of warblers - adults and juveniles -

survives annually and what is the reproductive success of warblers and cuckoos? What is the frequency of parasitism and the effect of brood-parasitism on the warbler's reproductive output?

(3) Measurements. How large an area do individual warblers and cuckoos occupy while breeding? What is the pattern of growth of nestlings?

(4) Description. How are warblers spatially and socially organised? What are nestling warblers fed? What are the causes of mortality of eggs and nestlings, and the mechanisms of parasitism?

As there have been few comprehensive studies of the breeding of small passerines or cuckoos in temperate Australasia I described in detail the warbler's nest-architecture (Appendix 2) and the development of nestling warblers (Appendix 3) and cuckoos (Appendix 4).

There is a great imbalance between the Northern and Southern Hemispheres in knowledge of the breeding of both passerines and brood-parasites. Studies of New Zealand passerines can make a special contribution to fundamental avian biology because they concern adaptive responses of birds to a special set of environmental conditions (remote oceanic location, depauperate fauna, original isolation from predators, evergreen vegetation, maritime climate). Field-work with cuckoos is often difficult and any fresh information on breeding must enhance our understanding of brood-parasitism.

Conventions

Throughout this dissertation, unless otherwise specified, "warbler" refers to *Gerygone igata* and "cuckoo" (in the specific sense) to *Chrysococcyx lucidus lucidus*. Reference to the Nest Record Scheme is to that of the Ornithological Society of New Zealand. Habitats 1, 2 and 3 are different kinds of forest at Kowhai Bush, described in the next chapter. Certain individual colour-banded warblers are referred to by the letters A to M (males) and the numbers 1 to 14 (females). Grey warblers are usually double-brooded. "Early" and "late" nests, eggs and young are those associated with a clutch started (respectively) before and after 23 October. All times are in New Zealand Standard Time (12 hours ahead of Greenwich Mean Time).

2. STUDY-AREA AND METHODS

2.1 STUDY-AREA

I did all field-work at Kowhai Bush (173°37' E, 42°23' S; NZMS1 S49 895 953), a strip of forest along the NE edge of the Kowhai River, 7 km NW of the peninsula and town of Kaikoura, in coastal SE Marlborough (South Island, New Zealand; Fig. 2.1). The forest, on alluvium, is a seral community dominated by kanuka (*Leptospermum ericoides*, Myrtaceae), and the density and diversity of native passerines is high by New Zealand standards. The forest is controlled by the Marlborough Catchment Board, and is tenuously connected to other native forest on the slopes of Mount Fyffe.

Kowhai Bush is an excellent area for studying forest-birds. It is close to a centre of population and a Field Station, from which it is readily accessible by road. The bush covers about 240 ha, and has clear boundaries. It is flat, so that such activities as mapping territories are not complicated by uneven terrain. The forest is a mosaic of distinct and sharply demarcated habitats, which represent successional stages. Differences between habitats added a further dimension to many aspects of this study. Most importantly, the canopy is low and in parts the forest has an open interior. Thus observing birds, and especially finding nests, was relatively easy. Further advantages of Kowhai Bush were the previous scientific studies (summarised by Hunt 1977), and the existing network of tracks.

Fig. 2.2 shows the section of Kowhai Bush between Schoolhouse and Postman's Roads. My main study-area of 30 ha comprised Habitat 2 and the block of Habitat 1 shown to the right of Floodgate Creek.

Climate

Kowhai Bush lies in an eastern climatic district (see Tomlinson 1976) characterised by moderate winters and very warm summers. The district experiences dry Foehn winds from the W which may produce day-temperatures in summer above 32°C. The other predominant winds are cool, wet southerlies and north-easterlies. The Kaikoura Peninsula receives an average annual rainfall of 865 mm on 134 rain-days, with an average of 2068 hours of sunshine per annum and an average temperature of 12°C (data from Kaikoura Meteorological Office, Ministry of Transport). Rainfall is heaviest in autumn (102 mm on average in May) and least in spring (51 mm on average in September). On average it is evenly distributed throughout the year, but in the short term it may

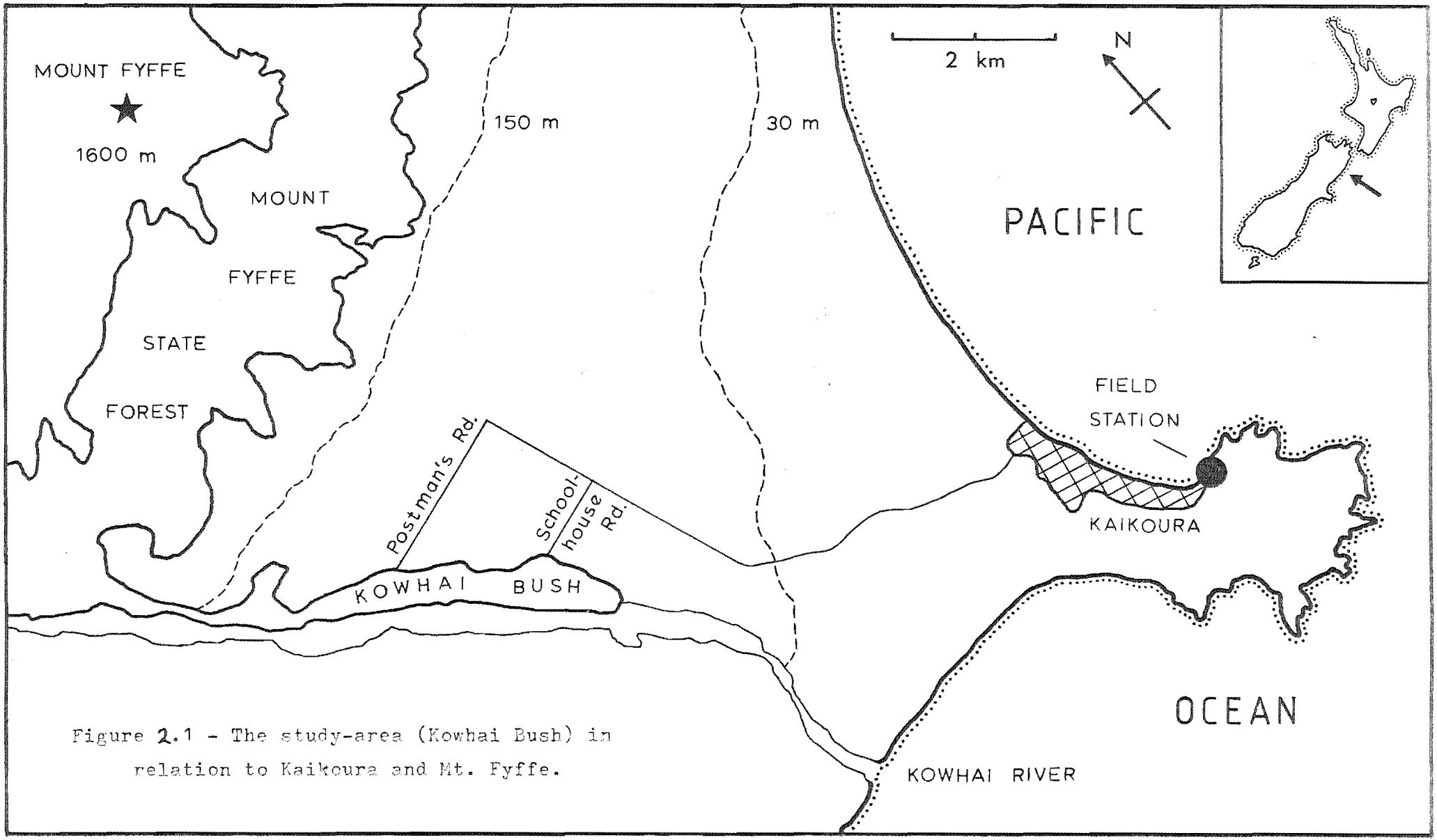


Figure 2.1 - The study-area (Kowhai Bush) in relation to Kaikoura and Mt. Fyffe.

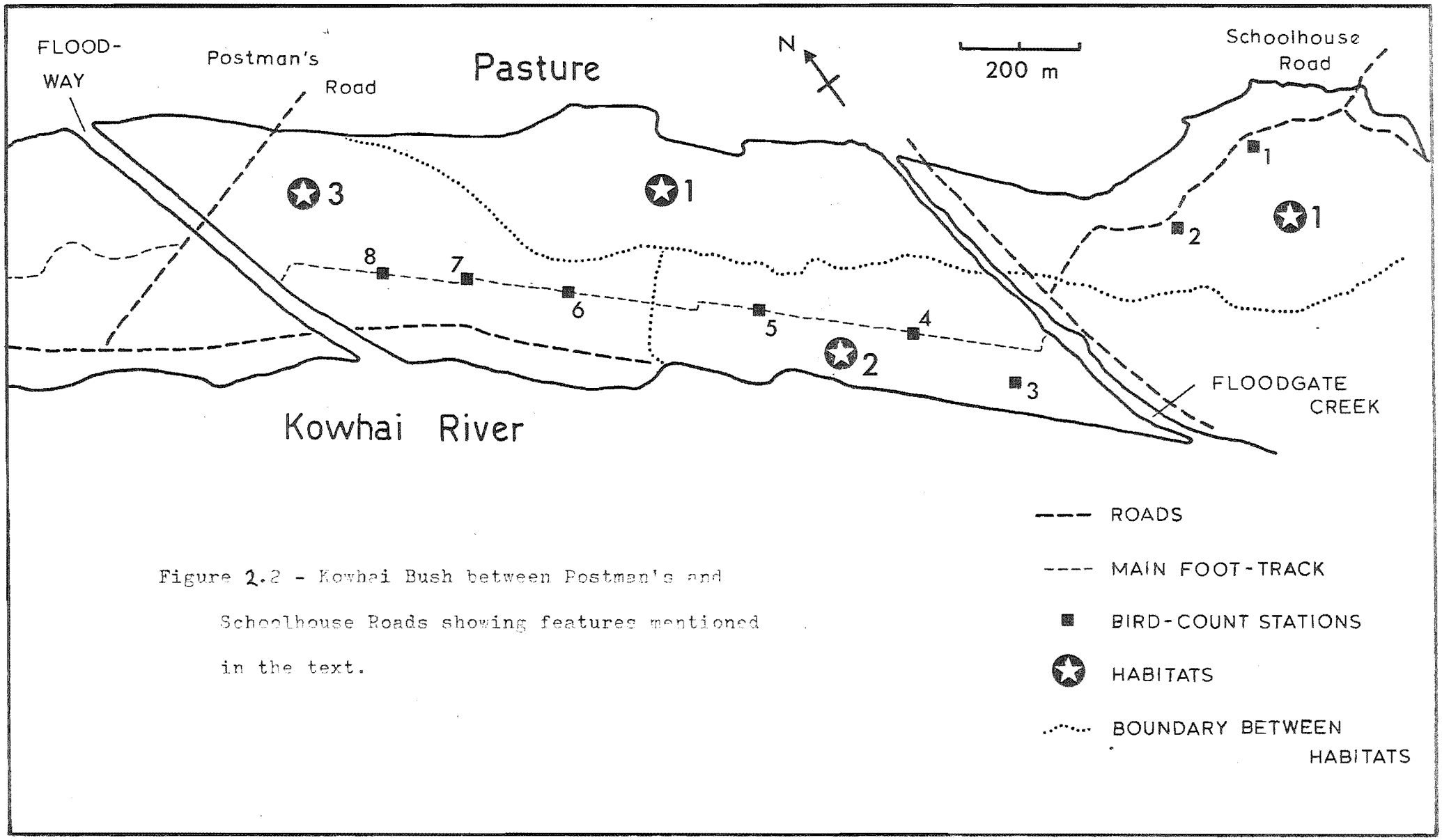


Figure 2.2 - Kowhai Bush between Postman's and Schoolhouse Roads showing features mentioned in the text.

vary erratically. The coldest month is July (mean temperature 7.4°C), and the warmest February (mean temperature 16.1°C). Kowhai Bush, being inland, has greater rainfall and more extreme temperatures than experienced on the Peninsula.

My study ran from early 1976 to early 1979 (inclusive). Winter 1976 was the coldest in the district for many years. Snow, which is extremely rare on the Kaikoura Plain, fell at Kowhai Bush during a 4-day southerly storm in late June, and it collected on ground not shaded by the canopy. Winters 1977 and 1978, by contrast, were wetter than usual. Summer 1976/77 was cool and wet, but the next two summers ended in drought.

Habitats

I recognised three habitats (Fig. 2.2) in the section of Kowhai Bush in which I worked. There was, of course, some variation within each, but in general they were distinct and sharply demarcated.

The habitats are as follows:

(a) Habitat 1. Stunted, open forest on stony soils (Plate 1A). Canopy, of *Leptospermum ericoides* with some *L. scoparium*, 5-12 m high ($\bar{x}$ = 7 m). No regular understorey, but small shrubs (notably *Pittosporum tenuifolium* and **Cytisus* spp.) and senescent *Coriaria arborea* scattered. Ground-cover of mosses, lichens, grasses, flatweeds, *Uncinia* and local expanses of *Phymatosorus diversifolius*. Shrubs in greater density and diversity occupy shallow gullies (possibly old water-courses) which traverse the area.

(b) Habitat 2. Tall, dense forest on silty-stony soils (Plate 1B). Canopy, of *L. ericoides*, 7-13 m high ($\bar{x}$ = 10 m). Understorey low, dense, and dominated by **Cytisus monspessulanus*. Other species in the understorey (notably *Coriaria arborea, Dodonaea viscosa, Melicytus ramiflorus, *Clematis vitalba* and **Ribes sanguineum*) scattered. Ground covered in grasses, *Uncinia*, herbs and ferns (ground-lichens absent, and mosses less common than in Habitat 1).

(c) Habitat 3. Very tall, dense forest on silty soils. Canopy, of *L. ericoides*, 10-15 m high ($\bar{x}$ = 12 m). Understorey tall, dense and diverse, with native species (*Dodonaea viscosa, Olearia paniculata, Pseudopanax arboreus, Melicytus ramiflorus*, and others) predominant and **Cytisus monspessulanus* unimportant.

Plate 1 - Habitats in the main study-area, Kowhai Bush.
(A) Habitat 1; ladder 4.5 m long.
(B) Habitat 2.

2.2 METHODS

"And I burnt my eyes with gazing. Still I see the poplars shiver,
Still I hear the little runnels down the folded gully falling,
But I never saw the bird!"

The Pipiwharauroa (Shining Cuckoo), Eileen Duggan 1929

I caught and marked about half the breeding adult warblers in the main study-area, and found about half the nests. I followed breeding intensively in 1976/77 and 1977/78 by visiting the study-area daily (mostly between 10:00 and 15:00h) from late July until late January. In 1978/79 I covered only the late half of the breeding-season closely, and monitored the early part intermittently.

Catching Adults

During autumn and winter I caught free-flying warblers in small mist-nets (5.5 m long; 2.1 m high) with 32 mm mesh (measured knot-to-knot with the netting stretched diagonally). Warblers sometimes passed through nets of 38 mm mesh. I hung the nets between two wooden poles (2 cm in diameter) held upright in short sections of square iron pipe driven part-way into the ground. A single guy-rope from the top of one pole usually kept the net taught. I set nets singly, or in pairs forming an "L"-configuration. With suitably long poles the net reached up to 3 m above ground and covered half to a quarter of the canopy's vertical height.

I netted on 50 days (May-August 1976, March-July 1977; 225 net-hours), and caught on average 0.3 grey warblers per net-hour. Some warblers entered the nets fortuitously, but most were lured by playing recordings of their song. I placed the tape-recorder to one side, with the speaker inclined towards the net. At other times I used twin extension speakers set one on either side of the net, and connected by a two-way switch which changed the sound from one speaker to the other instantaneously. A three-minute continuous cassette ("Philips CC-3") eliminated the need to re-wind tapes.

Adult shining cuckoos were easily attracted to recordings of their song, but I was unable to lure them down from the canopy into the net, even though I used a long net (17.5 m; 38 mm mesh).

During the breeding-season I caught 15 incubating female warblers on their nests using a fine hair-net mounted on a wire loop at the end of a stick. I caught birds only after they had been incubating for at least five days, and released them immediately after banding. None deserted.

Marking Adults and Nestlings

I banded 92 adult warblers and 96 nestlings. Each received a numbered metal band (size "A"; aluminium) supplied under permit by the Wildlife Service (Department of Internal Affairs) as part of the National Banding Scheme. I also gave each bird a unique combination of up to three coloured plastic "split"-bands (size "A"; cellulose), for individual recognition at a distance. Warblers have sufficiently long tarsometatarsi to carry three colour-bands on one leg. Reading colour-combinations was relatively easy using light (8 x 40) binoculars.

Nestlings of British song-birds are banded as soon as the remiges emerge from their sheaths (6-8 days old; Spencer 1965), but I banded warblers at a more advanced age (13-15 days). This was permitted by the long nestling period and disinclination of nestlings to fledge prematurely, and was necessary because bands slipped off younger nestlings.

As a further precaution against loss in the nest I compressed metal bands to a slightly oval, rather than round, cross-section. Once free-flying, warblers did not lose bands.

I banded nestling cuckoos (11) as soon as their legs were strong enough (12-15 days old). They took size "B" bands (aluminium and cellulose "splits"), but in some cases size "C" colour-bands would have fitted less tightly. The short tarsometatarsus of cuckoos takes no more than two colour-bands, and I did not try metal and coloured on the same leg. When cuckoos perch, little or no leg is visible, and reading colour-combinations was difficult.

Measurements

Under permit from the Wildlife Service I weighed and measured nestlings, and the warblers which I netted. For weighing I held adults head-downwards in small plastic bags folded to prevent struggling yet allow breathing through a hole in one corner. Nestlings, weighed in the same bags, needed little or no restraining. I used "Pesola" spring-balances of 10 g capacity (warblers and small nestling cuckoos) or 100 g

capacity (larger cuckoos). I measured wing-length (adults and some feathered nestlings) by holding the carpal flexure against a stop-plate rivetted to the zero-end of a ruler, and I measured other parameters with "Mitutoyo" stainless steel vernier calipers.

Plotting Territories

Sightings in the field, of banded warblers and cuckoos, were recorded in terms of paces to the nearest land-mark, and subsequently plotted on maps (original traced from aerial photographs held by the Marlborough Catchment Board, Kaikoura Office). The scale was 1 : 3960, and five paces in the field was roughly equivalent to 1 mm of map. The territory of a banded bird was the area within an outline enclosing all sightings of that individual from August to February (inclusive) in one season. I used the positions of disputes between neighbours as additional indicators of territorial boundaries. Each outline contained 4-34 well spaced sightings (mean = 16). I also considered the position of nests, and the area determined for a banded mate. I traced all territories for a season onto a single map and equally divided between neighbours any areas of overlap and narrow gaps between territories that could not have held other birds. To calculate areas I traced outlines onto graph-paper ruled in millimetres, counted the squares and converted to true area (1 mm^2 of map = 15.7 m^2 of territory).

Nests

During this study I saw 130 warbler-nests (Table 1.1), found by two methods:

a. by chance while walking through the forest or searching likely areas (sample biassed in favour of low, conspicuous nests), or

b. by following parent-birds (unbiassed sample with respect to height).

The surest way to find a nest was during building, by following the female who flies directly to the nest after collecting material. I found early nests under construction relatively easily because there was a long period during which most females in the population were building, accompanied by the vocal male. Late nests were harder to find because pairs bred out of phase, some replacing unsuccessful earlier nests, and others continuing uninterrupted. Late nests were built quickly and the female was hard to locate because she usually built unaccompanied by the male if there were fledglings of a previous brood, which he attended.

Table 2.1 - Numbers of nests seen during this study.

year	old or inaccessible	occupied	early	late	height: unbiassed	height: biassed	main study-area: inside	main study-area: outside	total
1976/77	19	38	22	16	16	22	23	34	57
1977/78	11	39	20	19	22	17	28	22	50
1978/79	2	21	12	9	14	7	16	7	23
total	32	98	54	44	52	46	67	63	130

I reached 55% of nests (n = 130) from the ground. To reach others I used an aluminium step-ladder extendable to 4.5 m (Plate 1A), and from which only 7% of nests were inaccessible. In the folded position the ladder (2.5 m long) was easily carried and manoeuvred within the forest. Once found, I marked the position of a nest with coloured plastic flagging. I measured dimensions with vernier calipers, height above ground with a tape-measure, and direction of entrance with a compass.

Eggs

I visited most nests once daily during laying and hatching, and regularly during incubation. I counted eggs by inserting one or two fingers through the entrance. During the months of parasitism I checked the identity of eggs daily (from laying to the 10th day of incubation) with a dental mirror (27 mm in diameter) mounted on a rod. No artificial lighting was necessary, and some low nests were such that the eggs were directly visible through the entrance.

Occasionally I removed eggs for weighing, measuring or marking, but this was too risky as a routine procedure. I marked eggs with one to four small dots made with an alcohol-based felt-tipped pen. Occasionally I accidentally broke or cracked an egg, but only once was this the apparent cause of a deserted clutch. Any eggs failing to hatch I opened to look for evidence of embryonic development.

Nestlings

I visited easily accessible nests once daily close to noon to weigh and measure nestlings. For broods of four I removed the nestlings in pairs and stood well away so that the parents could feed the remaining birds. I kept one nestling warm in a breast pocket while I handled the other. For smaller broods and cuckoos, which could be processed quickly, I often removed all at once and stood near the nest. No nests containing young were deserted on my account, so far as I was aware.

At the first visit after hatching I marked nestlings with red nail-varnish on the toes of one or both feet, leaving the last hatchling blank. This identified individuals in a brood until I banded them shortly before fledging. The varnish had to be re-applied every 3-4 days, though it lasted well on the claws of older nestlings. With care, I was able to weigh and measure nestlings even during the last few days of the nestling period.

Observations at Nests

To obtain frequencies with which parents fed nestlings, and to record the incidence of brooding, I sat near nests for 60 (occasionally 30) minutes at a time, in sessions between 10:00 and 15:00h. I did not use a hide; instead I sat quietly on a stool 15-30 m from the nest, often partly hidden in vegetation, and using binoculars. To feed nestlings grey warblers inserted only their heads through the entrance. The legs were always outside the nests, and it was easy to tell the parents apart if at least one was banded. I used a wrist-watch to record the temporal sequence of events, and a stop-watch to record the duration of events to the nearest 0.5 seconds. I watched nests only during fine weather (no rain or strong winds).

Composition of Nestling Warblers

To determine the composition of nestling warblers of known age, I used individuals that had died or been killed by predators. I removed stomach-contents from nestlings eight days or older. Fresh weights were not known in every case so I used the data in Table 6.5. I homogenised each nestling in its preservative (70% ethanol) using a "Waring" blender (with miniature cup and blades), slowly dried the homogenates in open jars on a hot-plate, and oven-dried them for three days at 60^{o}C to obtain dry weights. Fresh weight minus dry weight gave

the amount of water present. I ground the dried samples (weighing up to 1.7 g) with a pestle and mortar, and soaked them in petroleum ether (up to 100 ml per sample) for eight days to dissolve fat. I filtered the samples, oven-dried them for three days at 60°C, and obtained lean dry weights. Dry weight minus lean dry weight gave the amount of lipid present.

PART 1 - BREEDING OF THE GREY WARBLER

3. TERRITORIES

3.1 INTRODUCTION

Grey warblers apparently held self-contained all-purpose territories, the boundaries of which were determined through contest with neighbours, and to which were confined pairing, nesting and foraging. As with most birds (Lack 1968) warblers nested solitarily and were monogamous.

Of 40 free-flying warblers marked in the main study-area during winter 1976 (May to August), 15 (37.5%) later held territories and bred, six (15%) were sighted irregularly, and 19 (47.5%) were never seen again. Those lost from the population probably either died, or were juveniles hatched in 1975/76, which dispersed through the area unable to find vacant territory. Those sighted occasionally were probably either juveniles which lingered

before dispersing, or adults with summer territories just outside the main study-area. Those that later were territorial may have been adults already paired and established in the area.

In autumn and winter 1977 (March to July) I caught a further 12 birds in the main study-area, of which only three (25%) later held territories in the area. The catch was low and re-sightings few, apparently because residents in the area were habituated to my method of capture, so that most birds caught were dispersing and inquisitive juveniles.

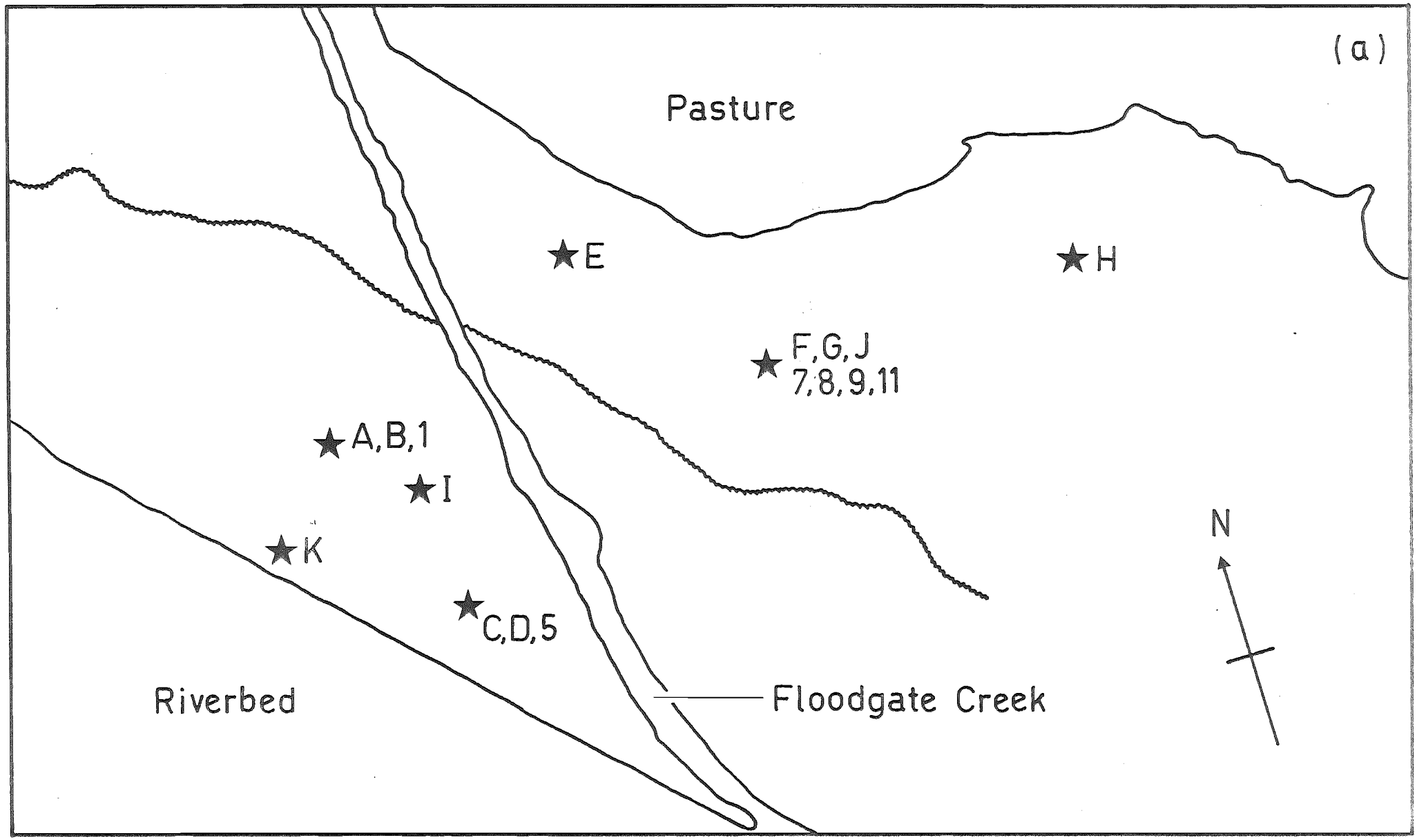
Much of the data in this discussion of territoriality and pairing are distilled into Fig. 3.1, which shows for banded individuals in three successive summers, the size, shape and position of territories in the main study-area, the positions of nests and the sites at which some birds were netted.

3.2 TERRITORIALITY

The banding of nestlings showed that during breeding (August to January) pairs drove from their nesting-areas any warblers other than their own dependent young. Banded members of breeding-pairs remained in one area of forest within which they collected material for nesting and apparently obtained enough food for parents, nestlings, and fledglings. Both sexes defended these territories against conspecifics, although males apparently more actively defended boundaries, while both sexes defended the nest's vicinity. Similarly, in most wood warblers (Parulidae) of North America the male defends the outer territory and the female guards a smaller area about the nest (Welty 1975).

Warblers settled most disputes at boundaries by chasing, rather than by physical contact. Agonistic sequences were extremely rapid, and I seldom identified antagonists, who, on encountering each other, chased in wide circles. Chasing often began with a spiralling flight up to 20 m above the canopy, and ended, several tens of seconds later, with the antagonists separating about 20 m from the starting point. Third and fourth birds who sometimes joined in were possibly females. A distinctive chattering call accompanied chasing, but whether given by pursuer or the pursued I could not tell.

Moderate overlap of adjacent territories is found with most species, and grey warblers seemed to trespass at any opportunity. Observations


(a)
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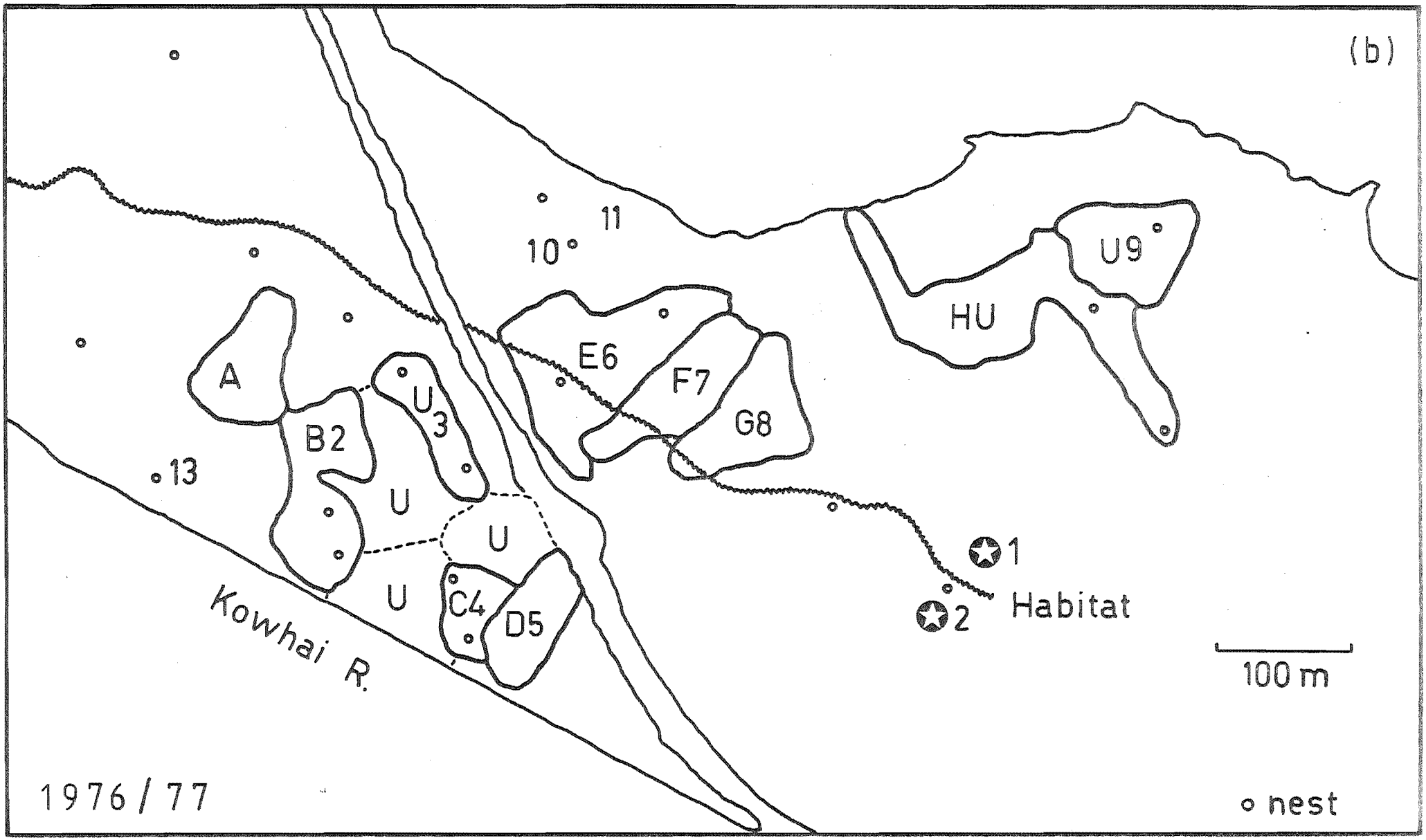
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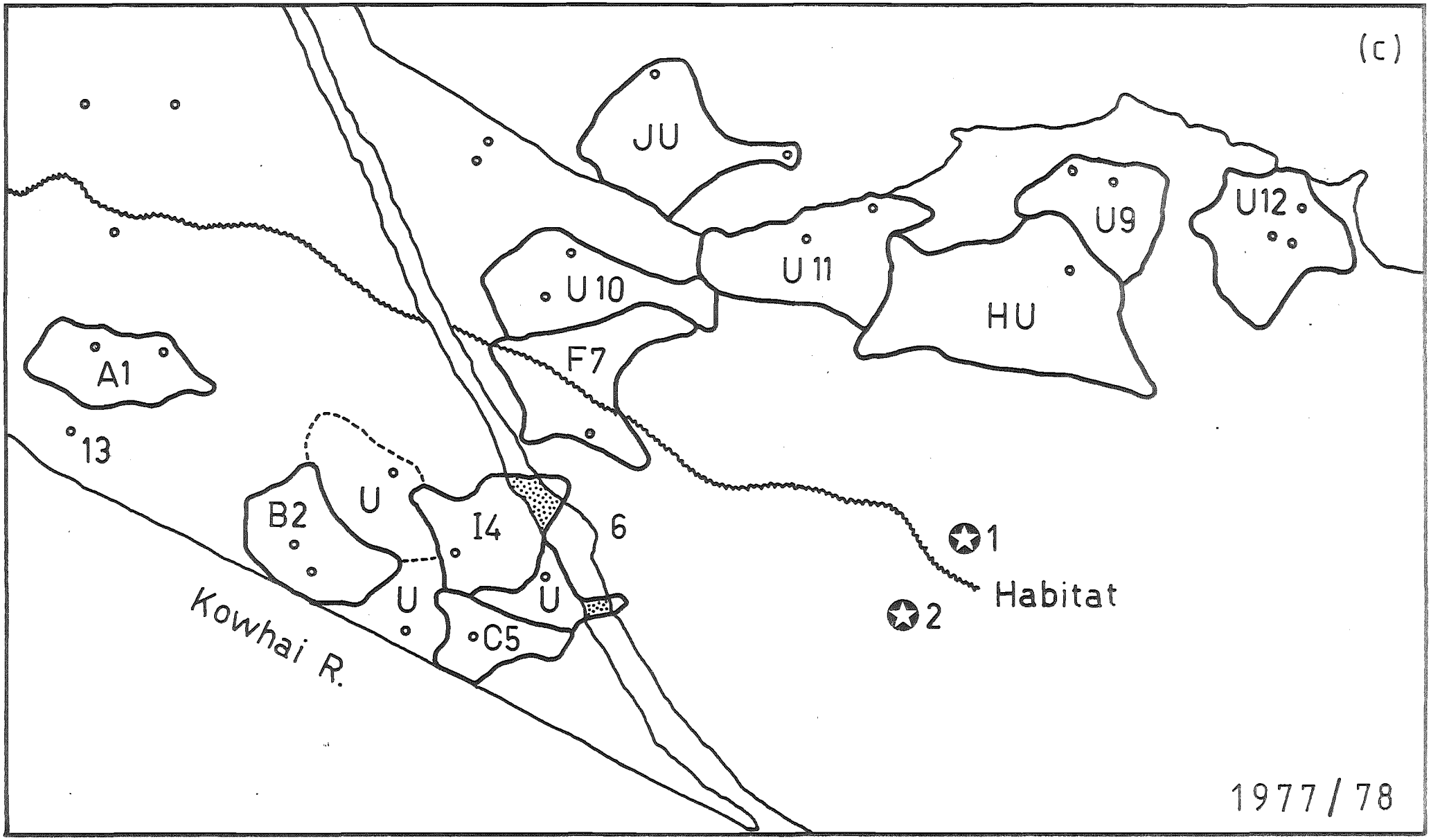
(c)
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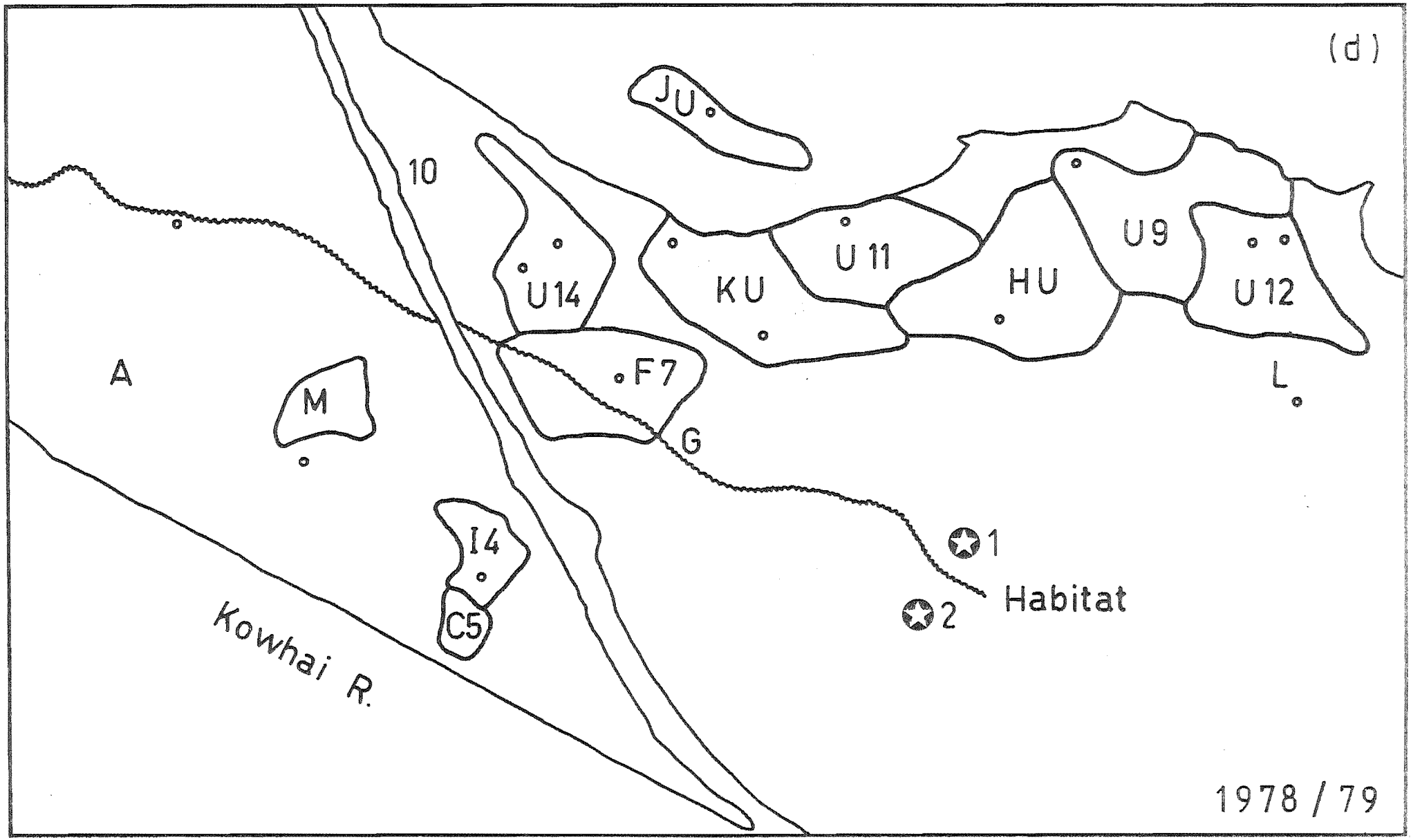
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Habitat
1978 / 79

at nests showed that nearly every pair contended with intruding warblers, who engaged the male's attention and, on approaching a nest, sometimes interrupted the rhythm of an incubating or brooding female.

Song (given only by male warblers) was doubtlessly of great importance in maintaining territories. It is typical of passerines in which the sexes are dull-coloured and similar that the male alone should sing, thereby allowing song to supersede sight in the recognition of conspecifics (Pettingill 1970). Full song increases through winter to a peak in September (Cunningham 1955 b; Fig. 8.1a), probably in direct reflection of increasing territorialism.

In winter when I lured warblers to nets, they gathered in groups of up to 12, and showed little intra-specific antagonism. Also, from March to July warblers often foraged in groups of 3-6, suggesting an absence or weakening of territoriality. Fig. 3.2 shows for three banded warblers, locations where in winter 1978 I saw them outside the territories that they nested in the following summer. Thus warblers appeared to occupy overlapping home ranges in winter which contracted into territories during the breeding-season. The home ranges were larger than territories, less distinct, and apparently uncontested, but they were in the same vicinity, emphasising the strict sedentariness of adults (section 3.3).

Groups of warblers in winter frequently contained one or a pair of birds that I knew to have bred, and they seemed to tolerate as associates other mature warblers, and juveniles. Where the latter were banded they had originated from distant nests, and were not the progeny of the banded adults.

3.3 SEDENTARINESS

Warblers in an area soon became habituated to the tape-recordings which I used (and did not change) during mist-netting. The catch fell to nil until I moved to a new site more than 100 m away, where the initial eager response was repeated. This suggested that birds were sedentary and that fresh individuals were involved at new sites.

Subsequent observations of banded birds bore out the impression. Many warblers with territories plotted in Fig. 3.1 b-d were caught in mist-nets, the positions of which are shown in Fig. 3.1 a. With the exception of ♂-K and ♀-9, all warblers held territories within about

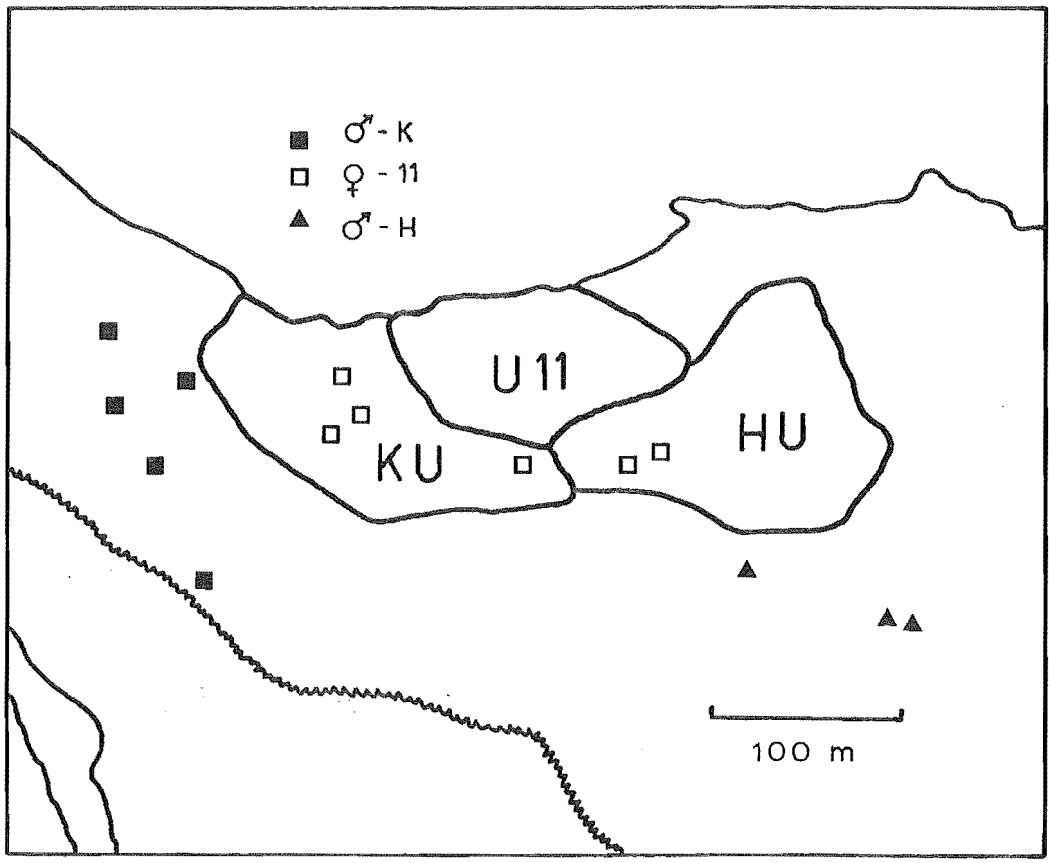

Figure 3.2 - Sightings in winter 1978 of three banded warblers (♂-K, ♀-11, ♂-H), in relation to their territories (KU, U11, HU) of the following summer.

100 m of the site at which I caught them in winter. Fig. 3.1 also shows that where I recorded the territories of an individual in two or three successive summers, the individual was tenacious to one area. In general, marked adult warblers recurred in a confined area throughout the year.

Changes in partner (section 3.5) or boundary (Fig. 3.1) always involved nearest neighbours. For example, ♂-F and ♂-E held adjacent territories in 1976/77, but with the absence of ♂-E the next year, ♂-F took over the area. In Habitat 2 the territories in a complex rearrangement between 1976/77 and 1977/78 (territories C4, D5, C5 and I4) were adjacent. No territorial changes involved shifts of more than about 100 m.

Most long-distance movements of banded warblers involved dispersing juveniles (section 7.3), which is what ♂-K, caught late in July 1977, probably was. Two weeks after banding, ♂-K had moved 400 m and occupied a territory, apparently as a bachelor, until late October. This is not shown in Fig. 3.1c because the area was subsequently divided between ♀-10 and ♀-11. However, ♂-K held a home range in winter 1978 (Fig. 3.2) and a territory the following summer (Fig. 3.1d) in the same area.

Adults of *Petroica australis* at Kowhai Bush are sedentary, and territoriality weakens only during the post-nuptial moult (Flack, in preparation). Similarly, fernbirds on the Snares Islands tend to spend the winter in the area of their previous territory (Best 1973).

In New Zealand no passerines migrate beyond the country, but some species move locally. Banding has shown that *Zosterops lateralis* may make long-distance movements, but the seasonal pattern is not clear (Kikkawa 1962). Indirect evidence from bird-counts suggests that in native forests near Reefton (Westland), varying proportions of the populations of some native passerines (including *Petroica macrocephala*, *Prosthemadera novaeseelandiae*, *Finschia novaeseelandiae* and *Gerygone igata*) may move altitudinally with season (Dawson *et al.* 1978).

Since forest continues from Kowhai Bush (effectively at sea-level) to about 1200 m on the slopes of Mount Fyffe (Fig. 2.1), this study was ideally suited to disclose any altitudinal movements of grey warblers. However, nearly 40% of the 40 birds I marked in winter 1976 remained in the main study-area to breed. Of the others, I saw only three the following winter, so it is unlikely that a major portion of the winter-population moves to higher altitudes to breed, and then returns to Kowhai Bush.

3.4 SIZES OF TERRITORIES

On average, grey warbler territories at Kowhai Bush were 0.68 ha (Table 3.1), the largest exceeding the smallest by seven times. Observations suggested that breeding warblers were denser in Habitat 2 than in Habitat 1.

Null Hypothesis: That on average warbler-territories in Habitats 1 and 2 were the same size.

Table 3.1 shows that territories in Habitat 2 were half the size of those in Habitat 1 on average. The difference is highly significant ($t = 5.60$ for 32 d.f.; $P < 0.001$) so I reject the null hypothesis.

Table 3.1 - Average area (ha) of warbler-territories at Kowhai Bush in two habitats; data for three breeding-seasons pooled. Combined value is the mean of means.

	$\bar{x}$	n	s	range
Habitat 1	0.915	19	0.313	0.51 - 1.73
Habitat 2	0.452	15	0.159	0.25 - 0.68
combined	0.684	34	0.344	0.25 - 1.73

The forest of Habitat 2 has a taller canopy, finer substrate and more dense and diverse understorey than that of Habitat 1, which grows on stony, dry soils, and is stunted with an open interior (section 2.1). The amount of vegetation per unit area is presumably greater in Habitat 2, and the supply of foliage-dwelling invertebrates on which warblers feed may vary accordingly. Thus territory-size and concentration of food may have been directly related. Similarly, Kluyver and Tinbergen (1953, cited by Brown 1969) found in Holland that three species of titmice (Paridae) were denser in mixed woods than in adjacent but less attractive pine-woods.

A direct relationship between territory-size and probable concentration of food at Kowhai Bush suggests that warblers existed there close to the limit set by food. If food was uniformly abundant,

then birds in the large territories of Habitat 1 might have had larger clutches than those at higher density in Habitat 2. (There was no evidence that birds in Habitat 1 had a longer laying-season than those in Habitat 2.)

Null Hypothesis: That average clutch-size did not differ between Habitats 1 and 2.

The mean clutch-size (years and early/late clutches combined) was 4.00 in Habitat 1 ($n = 17$) and 3.91 in Habitat 2 ($n = 21$). There is no significant difference (t-test; $P > 0.1$) so I accept the null hypothesis. This tends to support the suggestion that territory-size and food-concentration were directly related. Alternatively, there is a behavioural explanation of the density-vegetation relationship, as given by Best (1973), who found that territories of the fernbird on the Snares Islands were smaller where the vegetation was denser. In denser vegetation a male may see, hear and be heard over shorter distances, and may defend a correspondingly small area.

Table 3.2 gives the areas of individual territories at Kowhai Bush for which the male was the same in two or three years, or where, in that period, a male or female kept an unbanded mate. Also shown are yearly variations in average territory-size in the two habitats. In general, territories were uniform from year to year for habitats and individuals, except for a slight tendency to increase in size with successive years.

Table 3.2 - Area (ha) of territories of individual pairs (see Fig. 3.1). Means are for all territories properly measured in that habitat. Numbers of observations are bracketed.

Habitat	pair	1976/77	1977/78	1978/79
1 - stunted open forest	U12	-	0.80 (27)	0.87 (22)
	U9	0.58 (5)	0.58 (18)	1.18 (16)
	HU	1.26 (26)	1.73 (30)	1.28 (27)
	U11	-	0.96 (23)	0.82 (12)
	KU	-	0.64 (19)	1.14 (20)
	F7	0.58 (8)	0.86 (30)	0.98 (35)
	mean	0.82	0.91	1.00
	n	5	7	7
	s	0.36	0.39	0.21
2 - tall dense forest	C4/C5	0.25 (10)	0.36 (27)	0.14 (8)
	I4	-	0.59 (60)	0.30 (15)
	B2	0.75 (25)	0.68 (39)	-
	A/A1	0.49 (24)	0.56 (34)	-
	mean	0.47	0.48	
	n	6	7	
	s	0.17	0.17	
mean of means		0.64	0.69	

The strange shape of some territories (eg. B2 and HU; Fig. 3.1b) was probably an artefact of my not allowing for territorial changes during the breeding-season. However, the boundaries in relation to the positions of some nests are not necessarily suspect since some small passerines do not always nest at the centre of their territory (eg. May 1947). The nests of ♂-J (Fig. 3.1c,d) were in clumps of trees scattered among pasture where the nature of territoriality was unclear. Shape in this case was unreliable, and I excluded territory JU from considerations of area.

Kikkawa (1966) censused breeding warblers in native forests of the South Island by counts along transects. His data (in pairs/acres) suggest that on average, pairs occupied 4.5 ha (2.5-6.8 ha) in *Nothofagus*-forest, 2.2 ha (1.5-3.7 ha) in podocarp-forest, and 2.3 ha (1.6-2.9 ha) in low hardwood forest. These areas appear to be too large, suggesting that some birds were missed.

3.5 PARTNERSHIPS

Partnerships of banded warblers in successive breeding-seasons are given in Table 3.3 (to be read in conjunction with Fig. 3.1). Male-B and ♂-F each kept the same mate during two or three summers, and I often saw the males with their respective females at other times. Both ♂-B and ♀-2 disappeared from the main study-area in autumn 1978. The stability of these pairs is interesting since mating for life is rare among passerines (Lack 1968).

Male-G changed mates, but ♀-8 either died or moved away. Female-6 apparently deserted ♂-E during the second half of the 1976/77 breeding-season, but from June to August 1977 she occupied a home-range of 0.61 ha in the same area as her previous territory (Fig. 3.1b). Male-E was also present, but I did not see him after July 1977, and at the start of breeding in 1977 ♀-6 paired with an unbanded male 100 m away (Fig. 3.1c).

After the death or emigration of ♂-D, ♀-5 paired with ♂-C, while the latter's previous mate (♀-4) mated with ♂-I. Male-A apparently lost ♀-1 to an unbanded mate (with whom she nested) in the second half of the 1976/77 season, but ♂-A and ♀-1 paired again in 1977/78. Thus warblers at Kowhai Bush sometimes changed mates for reasons other than the death or emigration of a previous partner, though rarely within a breeding-season.

Table 3.3 - Pairing of banded warblers at Kowhai Bush for early and late halves of three breeding-seasons. U = unbanded bird; blank = no information; b = ♂ apparently a bachelor at that time; d = ♂ apparently died or emigrated.

	female					
	1976/77		1977/78		1978/79	
male	early	late	early	late	early	late
B	2	2	2	2	d	d
F	7	7	7	7	7	7
A	1?		1	1	U	
U		1				
C	4?	4	5		5	
D	5		d	d	d	d
I			4	4	4	
E	6	b	d	d	d	d
U			6			
G	8	8	U?		U	

3.6 SURVIVAL AND LONGEVITY

Of 21 warblers caught and banded in winter 1976, and which nested in the main study-area during summer 1976/77, at least 17 (81%) were also alive the next summer. Of 22 adults which bred in summer 1977/78, at least 18 (82%) were also alive during summer 1978/79. The average annual survival of adult warblers was therefore at least 81.5%, and the annual mortality 18.5% at most. Of the 21 marked warblers which bred in the first summer, at least 13 were still alive in the third summer, so survival over two years was at least 62%. Annual adult mortality in most temperate passerines is 40-70% (Farner 1955), but it may be 10-30% in tropical forest-species (Ricklefs and Bloom 1977). In this respect, therefore, grey warblers are like tropical wet-forest birds. At Kowhai Bush annual mortality of mated robins was about 20% (Flack 1973); for Malurus cyaneus near Canberra it was 34% (Rowley 1965).

Assuming (conservatively) that the 46 adults I netted in winter 1976 (or caught on nests early in the 1976/77 breeding-season) hatched on 31 January 1976, then, of the 46 originals: 13 that were alive at the start of breeding (August or later) in 1978 lived at least 2.5 years,

15 (33%) lived at least 2 years, and 21 (46%) lived at least a year. The longest-lived bird on the basis of sightings alone was ♂-H whom I saw 37 months after banding. However, assuming hatching in January, ♂-H lived at least 44 months, and eight birds (♂-A, ♂-C, ♂-F, ♂-G, ♂-H, ♀-7, ♀-9 and ♀-10) lived for 33 months or more.

The samples are small, but it seems regular for territorial warblers at Kowhai Bush to live three years. The average expectation of further life is $2 - m / 2m$ (eg. Gibb 1961), where $m = 0.185$ for warblers, the annual mortality. Thus life-expectancy for adult grey warblers that establish territories at Kowhai Bush is 4.9 years. The average expectation of further life for song-birds in the Northern Temperate Zone is only 1-2 years, though some may live up to 8-16 years in the wild (Thomson 1964). A banded *Gerygone chrysogaster* in Australia lived over eight years (Rydzewski 1977).

4. NESTS

4.1 DURATION OF BUILDING

Only female grey warblers collected material and built nests, as noted by Stidolph (1939). Among other small arboreal New Zealand passerines, both sexes of Bowdleria punctata and Rhipidura fuliginosa build, and two species of Petroica share the warbler's habit (Appendix 1). However, males of Petroica feed their mates during building, a phenomenon I never saw in grey warblers.

Seven early nests which I followed closely were built (and lined) in 16-27 days (mean = 22 days). Information from other nests between August and early October suggested that they were built in about three weeks, with a minimum of perhaps 12 days. The entrance and central cavity were formed after 5-10 days. Nests built in late October and in November I seldom found at an early stage. One, however, was completed in nine days, and five others took about a week, indicating that late nests were built three times faster than those earlier in the season. This is a common trend for species that breed more than once a year, perhaps because at the time of second nests they are more practised at building and food is more plentiful (Welty 1975). In general, then, it took a warbler 7-27 days to build.

Time spent building varies interspecifically with such factors as the nest's size and complexity, the materials used, and the role of the sexes (Welty 1975). Grey warblers may take up to four times longer to build than other native passerines (Appendix 1), but the female builds alone, without receiving food from the male, and the warbler's nest is heavy relative to the bird's size. Table 4.1 shows that the ratio of average nest-weight to mean adult weight is higher for grey warblers than for three other species at Kowhai Bush. The fantail's ratio may be halved since both sexes build (Appendix 1).

In Australia early in the season, the sexes of Acanthiza chrysorrhoa join to build an enclosed nest in 2-4 weeks, and in one week thereafter (Ford 1963). However, the female Malurus cyaneus builds an enclosed nest in only 3-4 days (Rowley 1965).

Table 4.1 - Weight (g) of nests and adults of four species of passerine at Kowhai Bush.

	nest-weight (A)			adult weight (B)		
	$\bar{x}$	n	range	$\bar{x}$	n	ratio A:B
grey warbler	9.7	23	5.6-18.0	6.4	50	1.52
brown creeper	11.2	6	9.0-14.0	13.1	10	0.86
fantail	8.7	6	6.1-11.0	7.9	17	1.10
chaffinch	14.5	5	13.0-16.5	c.22*	-	c.0.66

* breeding chaffinches in Britain (Newton 1972)

For early nests 2-8 days ($\bar{x}$ = 4.3 days, n = 12) separated the completion of building and the laying of the first egg. For three late nests, however, the delay was 1-2 days, and a warbler brought lining to a fourth nest containing the first egg (laid earlier that day). Thus, as with the duration of building, the delay before laying was shorter for late than for early nests.

Some other native muscicapids may also delay before laying for a week or more (Appendix 1). Similarly, many small Australian birds have long delays between building and laying - in Malurus cyaneus the interval is 5 days to a month (Rowley 1965); in Acanthiza pusilla it may be several weeks (Thomas 1974).

4.2 DATES OF BUILDING

Fig. 4.1 shows in weekly groups (beginning 21-27 July) the frequency with which I saw nesting material collected or nests built in 1976 and 1977. (The data are combined in Fig. 8.1.) Building began in late July or early August and continued until the final quarter of November. All first nests, or second attempts at building after an unsuccessful first nest, were completed by early October. New nests for true second clutches were started in late October or early November, but they were hard to find and I saw little building at this time. Although I probably overlooked building in early August 1976 because of inexperience, the data suggest that breeding was a week or two earlier in 1977 than in 1976, a trend confirmed in section 5.2.

Fifty-five cards in the Nest Record Scheme gave dates of building. The combined data (covering four decades) indicate building in every week from early August to late November. Seasonal bimodality in building was absent, obscured no doubt by the combination of years and localities. There were a few exceptional cases of building as early as the first quarter of June, and in late December, but generally accord was good between the dates for Kowhai Bush and for the country as a whole. A record in Classified Summarised Notes ("Notornis" 1(7): 79) reports building in early June. These early records are interesting since the shortest day is about 20 June. Thus warblers may build as days are getting shorter, which is unusual. In late July 1977, when I first saw warblers building at Kowhai Bush, day-length was about 9 hours 20 minutes, only some 10 minutes longer than on the shortest day, which emphasises that warblers breed early in the season.

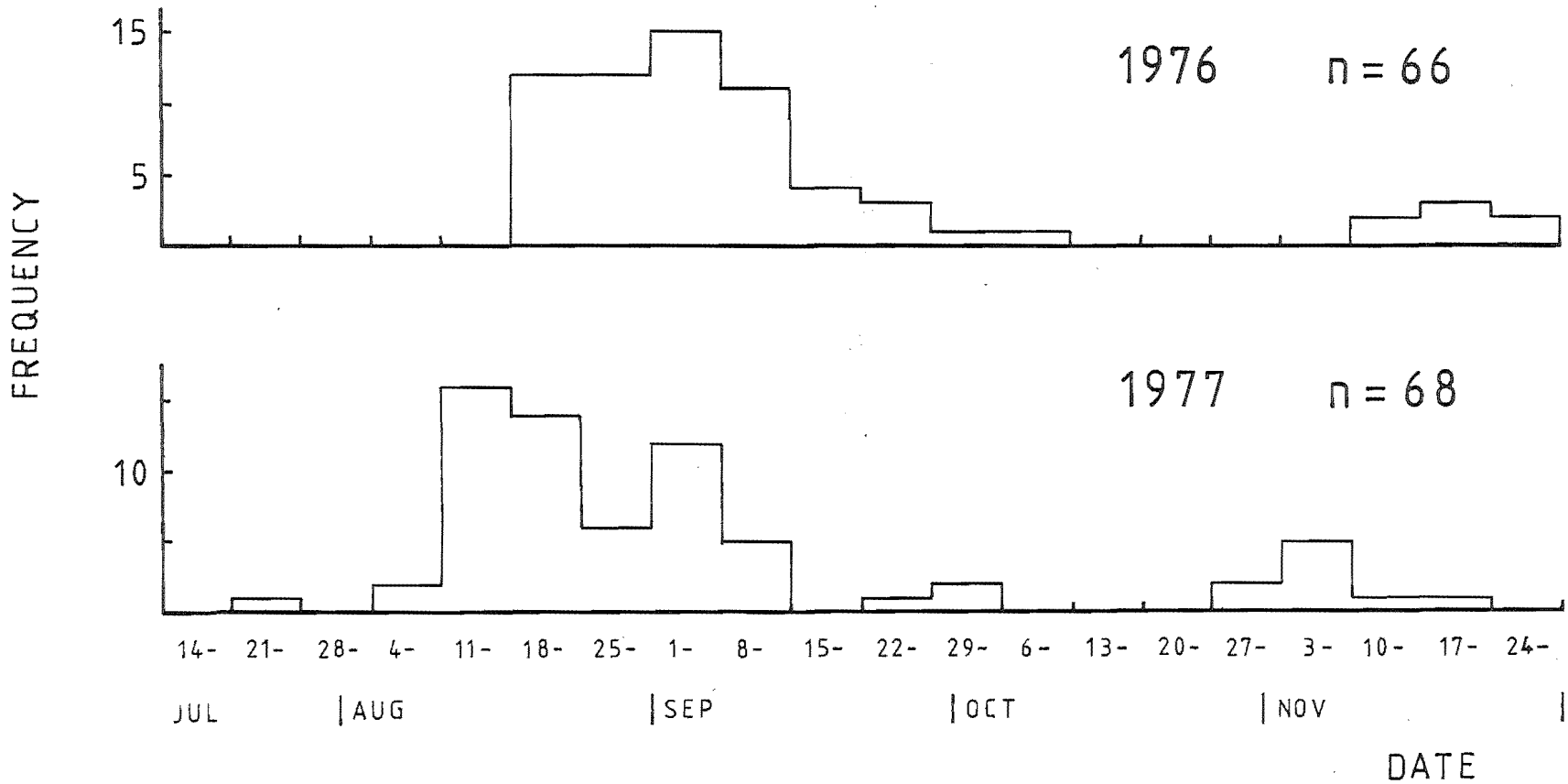

Figure 4.1 - Weekly frequencies with which I saw building at Kowhai Bush in two seasons.

4.3 DIRECTION OF ENTRANCE

According to Maori folklore grey warblers direct the entrances of their nests opposite to the direction of prevailing winds (Andersen 1926). To test this hypothesis I noted the orientation of entrances (Fig. 4.2) and compared the results with wind-roses for the Kaikoura Peninsula (frequency of winds of force 4 [Beaufort Scale] or stronger recorded at 09:00h for the four months during which warblers built [August-November]; data from Kaikoura Meteorological Office, Ministry of Transport).

Null Hypothesis: That the entrances to warbler-nests were randomly orientated.
Directions of entrances were significantly different from random in 1976 (χ^2 = 28.35 for 7 d.f.; $P < 0.001$) and for 1976 and 1977 combined (χ^2 = 31.80 for 7 d.f.; $P < 0.001$). However, directions did not differ significantly from random in 1977 (χ^2-test; $P > 0.1$). I therefore reject the null hypothesis for 1976 and for the total sample.

Null Hypothesis: That the frequencies of orientation of entrances varied in proportion to the frequencies of winds from the opposite directions.
(To test this prediction I had to group E-SE-S in 1976 and 1977, SE-S in 1976/77 combined, and SW-W-NW in every case.) The results for 1976 (χ^2 = 16.01 for 3 d.f.; $P < 0.005$), 1977 (χ^2 = 13.85 for 3 d.f.; $P < 0.005$) and 1976/77 combined (χ^2 = 124.58 for 4 d.f.; $P < 0.001$) show that in no case was there a significant all-round correlation between the orientation of nests and the occurrence of winds from the opposite direction.

Null Hypothesis: That entrances faced NE-E-SE or NW-W-SW in proportion to the frequency of winds from the opposite quadrant.
The result for 1976/77 combined (χ^2 = 5.14 for 1 d.f.; $P < 0.05$) causes rejection of the null hypothesis.

I conclude that although warbler-nests were often non-randomly orientated, the frequency and direction of winds were not directly responsible. Responses to solar insolation may be involved, though there was no obvious trend for either N- or S-facing entrances (Fig. 4.2). Alternatively, orientation may have been to specific aspects of the site involved, rather than to any gross environmental factor.

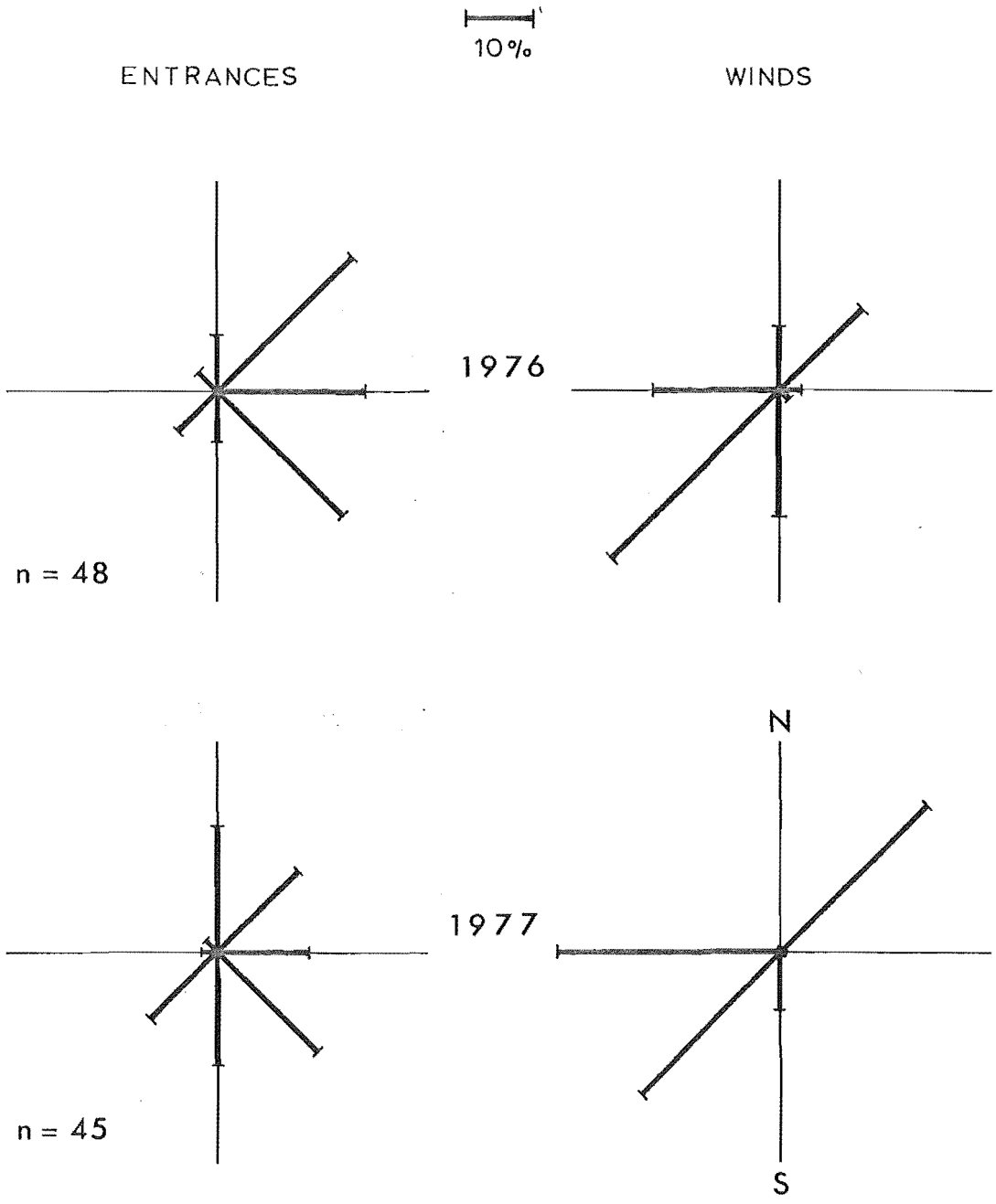

Figure 4.2 - Directions which entrances faced at Kowhai Bush, and from which winds blew on the Kaikoura Peninsula.

4.4 HEIGHT

At Kowhai Bush the height at which grey warblers nested seemed to vary between early and late halves of the breeding-season, and with habitat. To quantify and analyse these trends I measured the height of nests to the nearest 0.1 m, from their mid-point to the ground directly beneath. Where possible I measured the height of the tree or shrub involved; or estimated it, and the height of the canopy at that site, to the nearest 0.5 m. I combined data for 1976/77 and 1977/78, because the same trend was evident in both years. Except at the end of this section, I was able to pool the data for all three habitats and thus obtain a large sample, because the number of nests from each habitat was the same. Means were not therefore biassed in favour of any one habitat.

Nests found by following the owners formed a random sample with respect to height, while those stumbled upon by chance formed a sample biassed in favour of low nests. Also, I found fewer late than early nests Thus, the best average figure for nest-height is 3.5 m, the mean of the means for unbiassed early and late nests (Table 4.2).

Table 4.2 - Height above ground (m) of nests, trees nested in, and canopy at the site.

		$\bar{x}$	n	s	range
early nests	all	3.8	66	1.91	0.9-9.0
	unbiassed	4.5	29	2.06	0.9-8.5
	tree	5.1	60	2.47	1.2-11.0
late nests	all	2.1	37	1.38	0.7-8.0
	unbiassed	2.5	13	2.05	0.8-8.0
	tree	3.3	37	2.01	1.2-8.5
all nests	all	3.2	103	1.93	0.7-9.0
	unbiassed*	3.5	42	2.25	0.8-8.5
	tree	4.4	97	2.46	1.2-11.0
	canopy	9.5	94	2.61	4.4-17.0

* mean of two means

Null Hypothesis: That on average early and late nests were built at the same height in trees of equal stature.
Late nests were about 2 m lower on average than early ones (Table 4.2), and sited in shorter trees. The differences are significant: for early and late nests (all) $t = 5.36$ for 101 d.f. ($P < 0.001$); for unbiassed nests $t = 2.95$ for 40 d.f. ($P < 0.01$); and for trees $t = 3.78$ for 95 d.f. ($P < 0.001$). Therefore I reject the null hypothesis. Possible explanations of low nesting late in the season are avoidance of parasitism or seeking of shade.

The trend of the unbiassed heights (early versus late) is followed by the larger sample (Table 4.2), so I feel justified in using the latter in the following analyses of relative height. Table 4.3 and Fig. 4.3 show the height of nest in relation to that of the tree involved and the canopy at that site. Nearly all early nests were situated in the upper half of their trees, while late nests were lower on average with a much less skewed distribution of heights for reasons unknown. Similarly, Kikkawa (1966) found that blackbirds, song thrushes and silvereyes in Dunedin mostly built in higher parts of trees. Throughout the breeding-season, but especially in the second half, warblers at Kowhai Bush built low relative to the canopy.

The average height of the canopy at Kowhai Bush increased from 7.2 m to 9.7 m to 12.3 m (respectively) from Habitats 1-3 (Fig. 4.4). However, the mean height of nests was approximately uniform: 3.9 m in Habitat 1 ($n = 22$, $s = 2.10$), 3.1 m in Habitat 2 ($n = 24$, $s = 1.90$) and 3.5 m in Habitat 3 ($n = 19$, $s = 1.96$). The average ratio of nest-height to canopy-height (at that site) was 0.60 in Habitat 1, 0.36 in Habitat 2 and 0.34 in Habitat 3 (sample-sizes as above). Thus, where an understorey was absent (Habitat 1), warblers nested closer to the canopy than they did in denser forest.

Table 4.3 - Ratios of nest-height to tree- and canopy-height for early and late nests at Kowhai Bush.

		$\bar{x}$	n	s	range
nest:tree	early	0.75	60	0.175	0.20-1.00
	late	0.61	37	0.225	0.08-1.00
	all	0.70	97	0.207	0.08-1.00
nest:canopy	early	0.45	58	0.284	0.08-1.00
	late	0.27	36	0.226	0.06-0.94
	all	0.38	94	0.278	0.06-1.00

4.5 PROXIMITY

Fig. 3.1 shows the spatial arrangement of nests found in the main study-area. Given the smaller average territory-size in Habitat 2 (section 3.4) one would expect nests to be closer together there than in Habitat 1.

Null Hypothesis: That on average early and late nests of a pair were the same distance apart in Habitats 1 and 2. Average distances between early and late nests of a pair were 47 m (n = 15, s = 29.5, range = 16-111 m) in Habitat 1 and 48 m (n = 5, s = 23.2, range = 26-85 m) in Habitat 2. The difference is not significant (t-test; $P > 0.2$) so I accept the null hypothesis. Grey warblers may build their nests a certain distance apart that is not restricted by the relative smallness of territories in Habitat 2.

Null Hypothesis: That on average concurrent nests of different pairs in adjacent territories were the same distance apart in Habitats 1 and 2. Concurrent nests of neighbouring territories were closer in Habitat 2 ($\bar{x}$ = 72 m, n = 10, s = 11.0, range = 57-95 m) than in Habitat 1 ($\bar{x}$ = 112 m, n = 14, s = 23.5, range = 71-154 m), the difference being highly significant (t = 5.56 for 22 d.f.; $P < 0.001$). Therefore I reject the null hypothesis. With larger territories in Habitat 1, neighbouring pairs built further apart than in Habitat 2.

Clearly, both the height of warbler-nests (section 4.4) and their spatial arrangement may vary significantly between even very similar habitats.

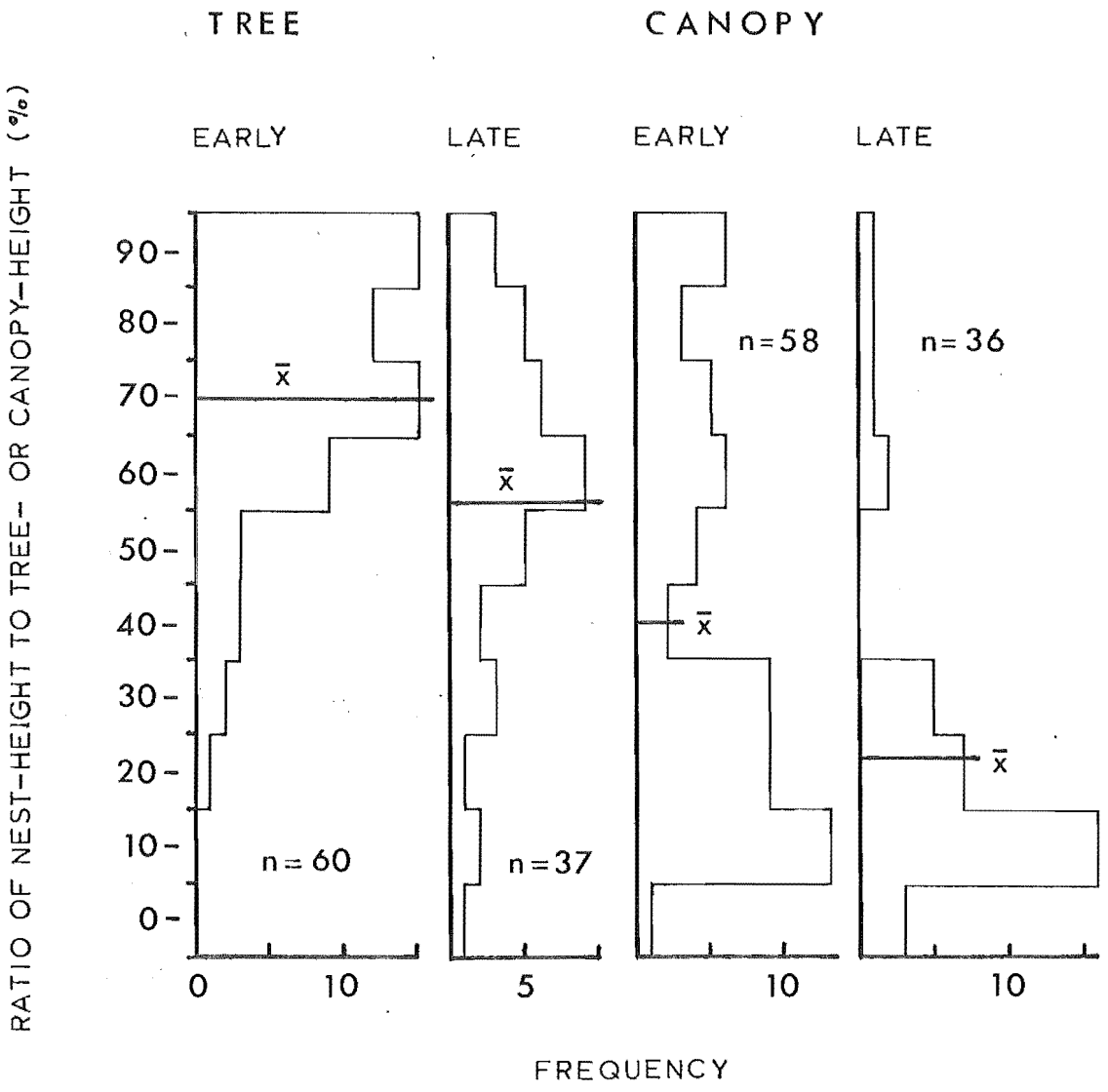

Figure 4.3 - Height of nest in relation to height of tree and canopy for early and late nests at Kowhai Bush.

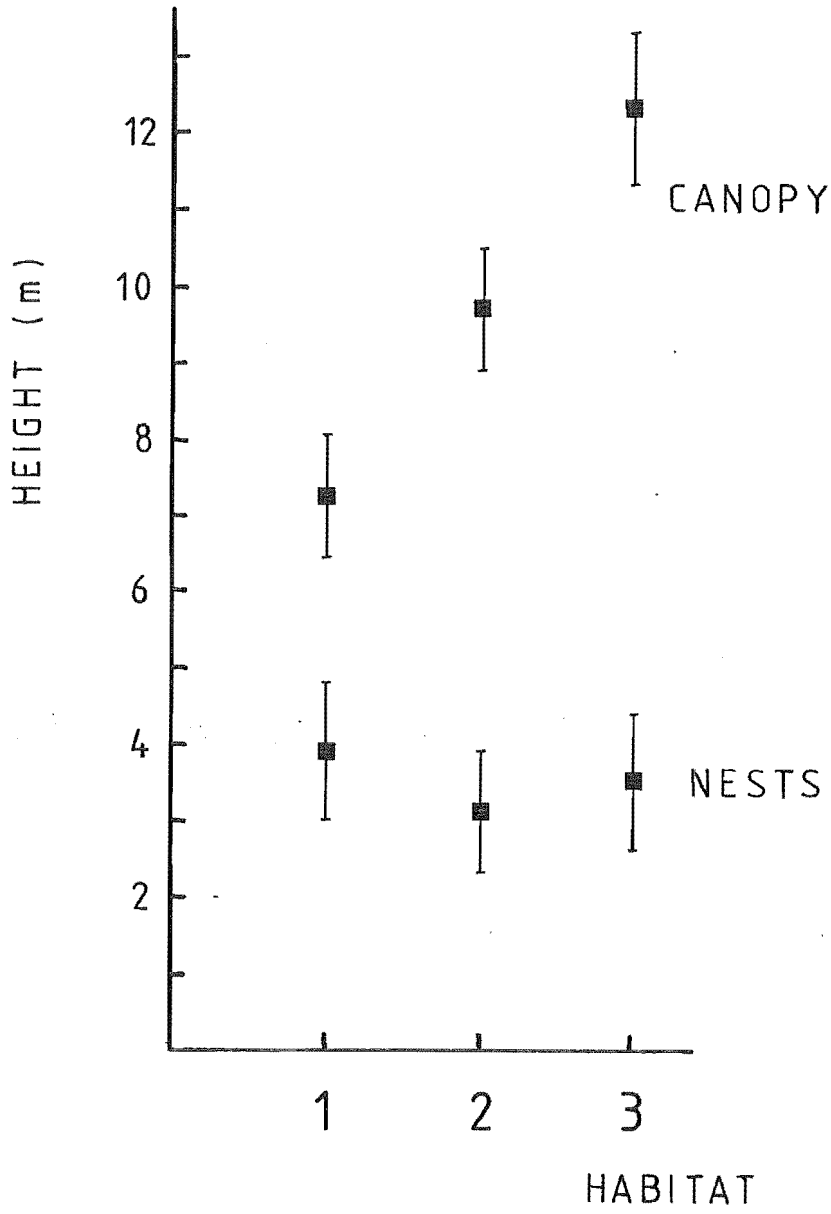

Figure 4.4 - Height of canopy and nests in three habitats at Kowhai Bush; mean ± 2 SE.

5. EGGS

5.1 COPULATION

I saw copulation of grey warblers six times (between late October and mid-December). In one instance copulation preceded the first egg of the clutch by 14 days. Another pair copulated on about the same day they produced the first egg (nest undiscovered at the time); another on about the day they laid the third egg of four. One instance of copulation (apparently without avail) preceded moulting in the male by only a month.

Mounting lasted less than 10 seconds, but was usually repeated, the male alternately balancing on the female's back by constantly fluttering his wings, and perching beside her. The female displaced her tail to the left (two instances) for cloacal contact, and sometimes held nesting material or food in her bill. A harsh chattering was given, at least on one occasion by the female. Birds copulated on the ground or on perches, some nearly vertical.

5.2 DATES OF LAYING

The dates of laying of individual eggs are shown for 1976/77 and 1977/78 separately (Fig. 5.1) and combined (Fig. 8.1). Where I did not know the date of laying exactly I estimated it as follows:

a. from the known interval between deposition of eggs in a clutch (section 5.4), given the laying-date of a later or earlier egg;
b. from a known date of hatching and the average incubation period (section 5.8);
c. from the age of a young nestling (estimated from weight; Table 6.5), and the average incubation period; or
d. from a known date of fledging and the average nestling period (section 6.4) and incubation period.

These estimations introduce no serious error when the data are grouped by weeks (Cramp 1955).

At Kowhai Bush the laying-season of grey warblers was 15 or 16 weeks (Fig. 5.1), between the last quarter of August (earliest egg 25.viii.1977) and the third quarter of December (latest egg c. 17.xii.1976). The distribution was bimodal, reflecting the two broods per season which a pair can raise successfully. Since I did not find every nest of all

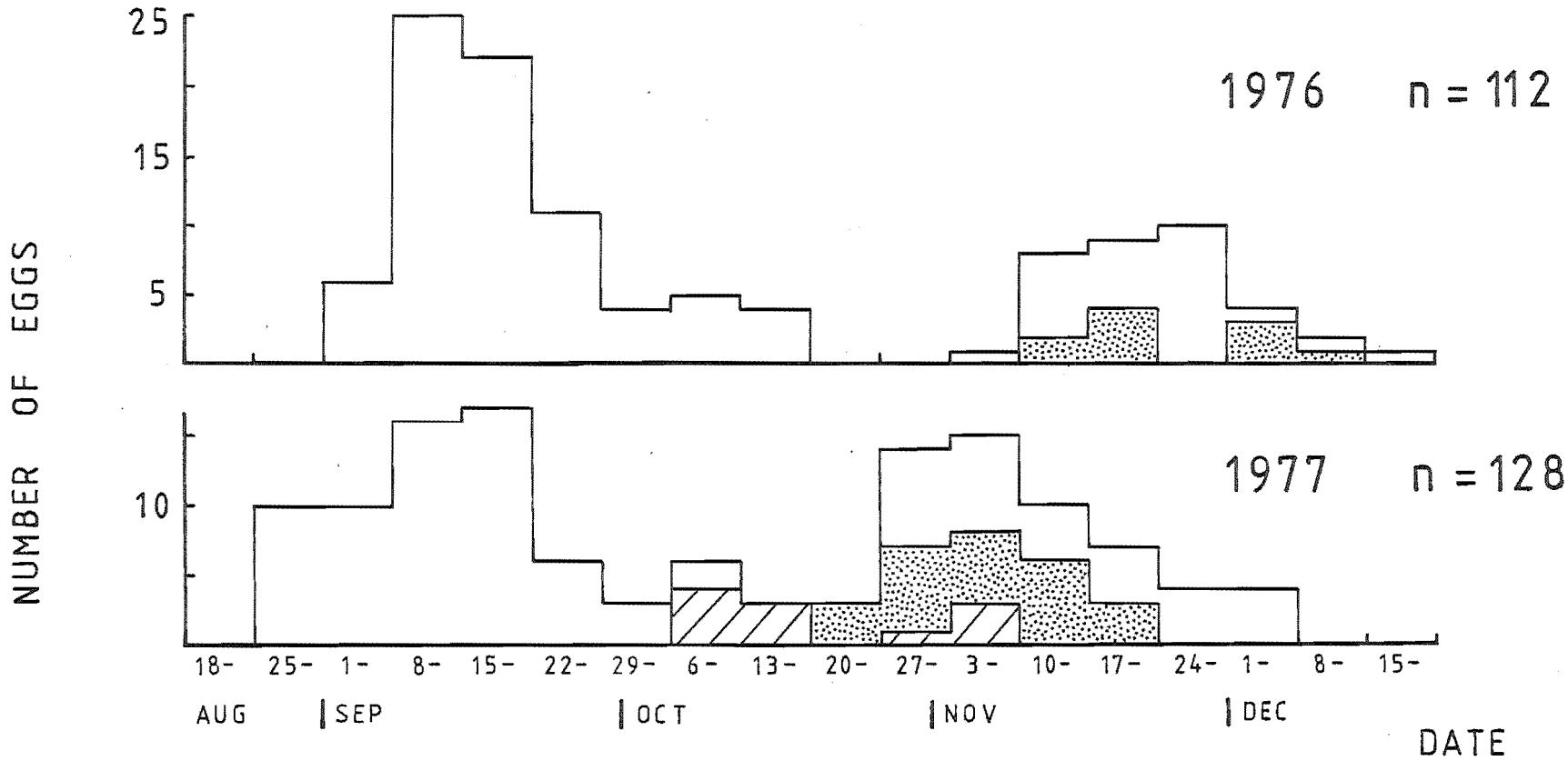

Figure 5.1 - Dates of laying of warbler-eggs at Kowhai Bush, grouped into weeks.

pairs in the study-area, from late September onwards it was not always possible to know whether a clutch followed a successful or unsuccessful earlier nest (or any nest at all). Repeated clutches after loss of a first, and true second clutches (following the fledging of at least one nestling from the earlier brood) are indicated in Fig. 5.1 where known. The earliest egg of a true second clutch was laid on 23.x.1977. For convenience I considered all clutches initiated after this date as "late", and those started before as "early".

Late nests were hard to find (section 2.2), so it is unlikely that there were fewer late than early clutches as Fig. 5.1 suggests. Warblers apparently laid earlier in 1977 than in 1976, though my greater experience at finding nests in the second year may have biassed the results slightly. However, information from banded birds supports the trend. Table 5.1 gives dates of completion of corresponding clutches in two years, for pairs with at least one partner banded. In all five cases laying was earlier in 1977, by 7-20 days. The cold winter and cool, wet spring of 1976 (section 2.1) may have adversely affected the warblers' food-supply and delayed laying.

Table 5.1 - Dates of clutch-completion for banded individuals in two years (U = unbanded bird; * = late clutches, all others early).

		date of clutch-completion		
♂	♀	1976	1977	difference (days)
U	9	19.ix	12.ix	7
H	U	27.ix	14.ix	13
U	13	16.ix	5.ix	11
B	2	17.ix	31.viii	17
B	2	*9.xii	*19.xi	20

Fifty-five cards of the Nest Record Scheme, covering five decades and localities throughout New Zealand, together indicated laying in every week from mid-August to early December. This conforms with the pattern at Kowhai Bush, but a few cards gave exceptional cases of laying in mid-June, July and early January.

Observations of banded warblers during August and September, or of unbanded birds in particular localities, showed that the onset of laying

was asynchronous, and that some females laid their first clutches in late September (and perhaps early October), as much as five (or six) weeks after the earliest breeders. Similarly, fernbirds on the Snares Islands lay first clutches in 8-11 weeks (Best 1973).

Petroica australis at Kowhai Bush begins laying earlier than warblers. Taking 1 July as day 1, in 1977 the average day of clutch-initiation in robins was 46.7 or 16 August (range = 23-61; R. Powlesland, pers. comm.), compared with 70.0 or 8 September for warblers (range = 56-83). Silvereyes in Auckland, however, do not start laying until early October (Fleming 1943). On the sub-antarctic Snares Islands, *Bowdleria punctata* laid during 13 and 16 weeks in two seasons, beginning early November (Best 1973) - two months later than warblers. However, near Nelson, fernbirds started and finished breeding earlier than on the Snares Islands, and they laid during 22 weeks (Elliott 1978).

Acanthiza chrysorrhoa in south-western Australia usually lays from early July to December (Ford 1963), and at Canberra *Malurus cyaneus* starts clutches from mid-August to early February (more usually early September to early January; Rowley 1965). Thus the long period of laying and its early start are also characteristic of the grey warbler's close relatives in Australia.

5.3 TIME OF LAYING

Passerines typically lay in the early morning, often between first light and sunrise (Pettingill 1970). Three early warbler-eggs at Kowhai Bush were laid within an hour of first light, probably, in two cases (Table 5.2), a few minutes after sunrise. However, card-6435 of the Nest Record Scheme reports the laying of a fourth and final egg between 08:00 and 16:00h on 30.xi.1967.

Table 5.2 - Observations at a nest in September 1977 during laying of the third and fourth (final) eggs of a clutch. First light c. 06:00h; sunrise 06:40h; all times in minutes.

date	♀ entered nest	period in nest before laying	presumed start and duration of laying	period in nest after laying	♀ departed nest	total period in nest
12	06:36h	9	06:45h (1.5)	7.5	06:54h	18
14	06:29h*	25.5	06:54.5h (1)	9	07:04.5h	35.5

* ♀ was flushed from nest at 06:14h but returned at time shown

5.4 LAYING-INTERVAL

Passerines typically lay eggs of a clutch 24 hours apart (Welty 1975). Outside Australasia the only known exceptions are some Formicariidae, Tyrannidae and Pipridae which lay at 48-hour intervals (Lack 1968). All belong to the sub-order Tyranni. The only song-birds (sub-order Oscines) known to lay at 2-day intervals are Australasian. Courtney and Marchant (1971) reported it in the Cracticidae and in *Smicrornis brevirostris*, *Acanthiza reguloides*, *A. chrysorrhoa*, *Gerygone olivacea*, *G. fusca* and *G. richmondi*. Thomas (1974) added *Origma rubricata*, *Sericornis frontalis* and *Acanthiza pusilla* to the list - all these small passerines are close relatives of the grey warbler.

At Kowhai Bush in two seasons, 67 eggs of the grey warbler followed two days after the preceding egg. The only apparently genuine exception was the third egg in an early clutch of three, which appeared to be laid three days after the second egg. Either that, or it was laid after my visit at 11:30h on the day it was expected. Only five cards of the Nest Record Scheme gave laying-intervals. All were of two days except for cases where the first egg of three, and third egg of four, were apparently three days in the nest before the next egg was laid.

5.5 COLOUR, MEASUREMENTS AND WEIGHT

Eggs of the grey warbler were white with reddish-brown speckles (Plate 2).

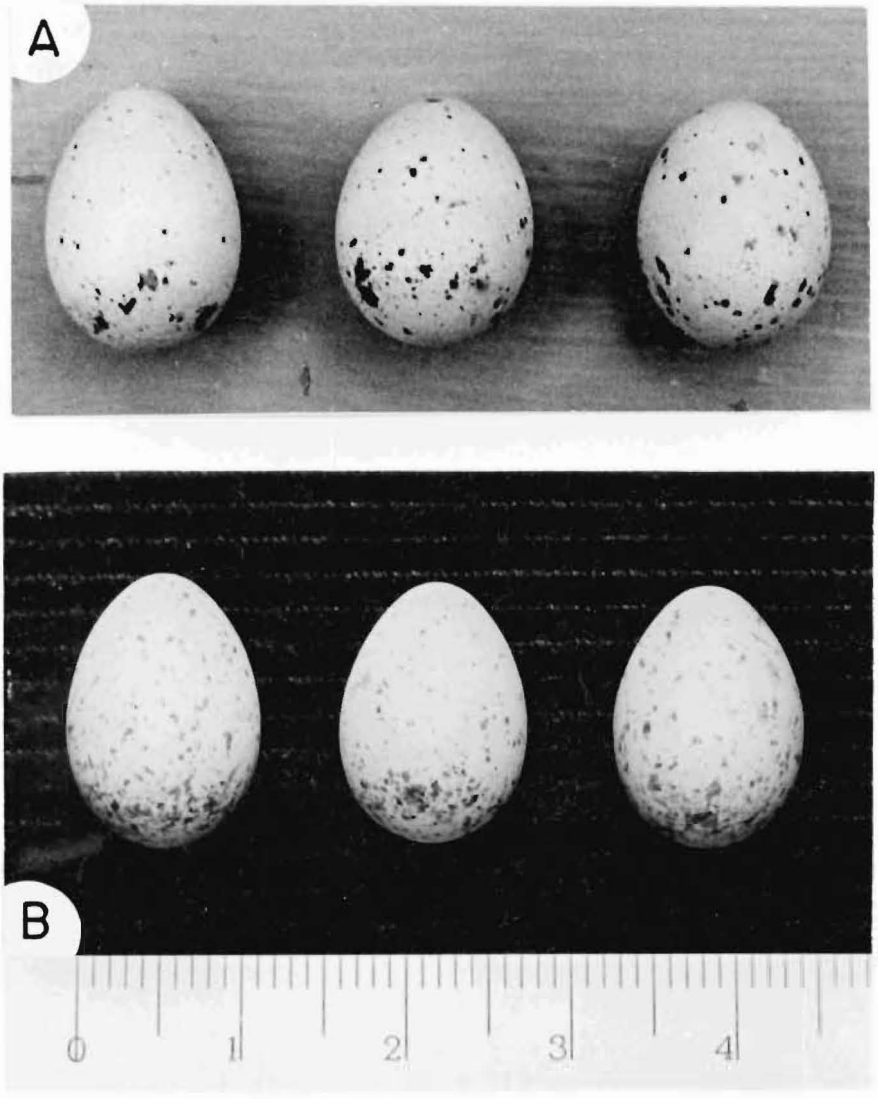

Plate 2 - Warbler-eggs from two clutches showing variation in pattern. (A) Large-speckled eggs. (B) More typical, finely-speckled eggs; scale in mm.

Birds with open nests usually have cryptically coloured eggs, while eggs of hole-nesters are often pale, suggesting the loss of a character with no advantage, or selection for enhanced visibility (von Haartman 1957). Some Turdinae with nests of intermediate concealment in shallow holes or niches have white eggs with reddish-brown speckles, which Lack (1958) suggested might represent a compromise between the advantages of visibility to the parent birds and invisibility to predators.

The New Zealand Muscicapidae comprises seven species with cupular nests, two with enclosed pensile nests (eg. the grey warbler), and one species nesting in holes. However, all have white or cream-coloured eggs with red, brown or purple speckles, often concentrated at the larger end (see Falla *et al.* 1970). Thus colour of egg and type of nest are unrelated in this group.

I measured warbler-eggs in the field at Kowhai Bush to the nearest 0.05 mm. On average they were 17.1 x 12.1 mm (Table 5.3). The longest egg (18.8 x 11.4 mm) was nearly the narrowest, and the shortest (15.8 x 12.8 mm) was nearly the widest, but there was no statistical correlation between length and width ($r^2 = 0.01$, $n = 35$). On average eggs were 5.8 mm shorter and 4.6 mm narrower than those of the fernbird (Best 1973), and they probably rank equal with those of *Acanthisitta chloris* as the smallest of any New Zealand bird.

Early eggs of Petroica australis at Kowhai Bush tend to be larger than later ones (R. Powlesland, pers. comm.).
Null Hypothesis: That on average, warbler-eggs from early and late clutches did not differ in size.
Early warbler-eggs were 16.95 mm long on average ($n = 16$, $s = 0.638$), compared with 17.21 mm ($n = 15$, $s = 0.895$) for late eggs, the difference being not significant (t-test; $P > 0.1$). However, the difference in width between early eggs ($\bar{x} = 11.96$ mm, $n = 17$, $s = 0.381$) and late eggs ($\bar{x} = 12.23$ mm, $n = 15$, $s = 0.362$) is highly significant ($t = 5.50$ for 30 d.f.; $P < 0.001$). I therefore reject the null hypothesis.

Table 5.3 - Dimensions (mm, mm^3) of warbler- (W) and cuckoo-eggs (C) from Kowhai Bush.

		$\bar{x}$	n	s	range
length, L	W	17.08	31	0.772	15.75 - 18.80
	C	18.68	4	1.124	17.30 - 20.05
width, B	W	12.08	32	0.391	11.30 - 13.00
	C	12.63	4	0.562	12.00 - 13.10
volume-index, LB^2	W	2498.55	31	207.155	2094.12 - 2999.75
	C	2990.16	4	414.846	2491.20 - 3440.78

The mean weight of nine warbler-eggs taken (to the nearest 0.05 g) within about six hours of laying was 1.49 g (s = 0.08, range = 1.40-1.60 g) or 23.3% of the mean adult weight (6.4 g). According to the regression-curve in Lack (1968: 184), passerines of 6.5 g have eggs that are individually about 13.2% of their weight. Thus eggs of the grey warbler are much heavier than expected for a bird of its size. My value for adult weight is for sexes combined in winter, and breeding females may be heavier. However, it is inconceivable that they could weigh the 11.3 g that would make their eggs 13% of body-weight. (An incubating female weighed 6.8 g in October 1978.) The weight of the fresh egg is known for only two other native passerines. The data for *Acanthisitta chloris* are identical to those for the warbler (egg 1.5 g or 22% of adult weight; Gaze 1978), while in *Petroica australis* the egg is 4.7 g or 13% of the female's weight (35.1 g; Flack, in preparation). Overseas the eggs of Gerygone chrysogaster and G. palpebrosa are about 1.5 g (Schönwetter 1964) and adults weigh about 9 g (Diamond 1972) so the eggs are about 17% of adult weight.

The weight (W), length (L) and width (B) of avian eggs are related according to the expression $W = k\ L\ B^2$. Substituting average values for grey warblers, k (for fresh eggs) = 1.49 g/1.708 cm $(1.208\ cm)^2$ = 0.598. Romanoff and Romanoff (1949) gave k as 0.546 for 14 altricial species.

5.6 CLUTCH-SIZE

Table 5.4 shows that 90% of clutches contained four eggs, and that the average size was 3.93. Clutches of three and five were rare. In addition to the data shown there were two apparent clutches of two, and further clutches of three, but these probably resulted from loss of eggs during laying or incubation. In the Wairarapa, Stidolph (1939) found no more than four eggs per warbler-nest; four or three being the usual numbers, with occasional clutches of two, especially late in the season. In the Nest Record Scheme 91 cards reported nests with four eggs or less and there were only two records of 5-egg clutches (up to and including card-12267, 1978).

Table 5.4 - Frequency of clutch-sizes (percentage frequency in brackets) and mean clutch-size; data for three seasons combined.

	clutch-size					
clutch	5	4	3	$\bar{x}$	n	s
early	1 (2.6)	36 (92.3)	2 (5.1)	3.97	39	0.280
late	0	18 (85.7)	3 (14.3)	3.86	21	0.359
total	1 (1.7)	54 (90.0)	5 (8.3)	3.93	60	0.312

In some species of song-birds average clutch-size may change during the breeding-season.

Null Hypothesis: That on average early and late clutches of grey warblers did not differ in size.

The difference in mean size of early and late clutches (Table 5.4) is not significant (t-test; $P > 0.1$) so I accept the null hypothesis. Clutch-size in warblers is remarkably constant.

Passerines with nests relatively secure from predation (especially hole-nesters), tend to have larger clutches than those with cupular nests (Lack 1948, von Haartman 1957). New Zealand passerines seem to follow this trend (Appendix 1); average clutch-size increases from fernbird/robin/fantail to warbler to rifleman as the nest changes from cupular to enclosed to contained within a hole.

Many small passerines of temperate Australia have slightly smaller clutches than the grey warbler: mean clutch-size is 3.7 (range = 3-4) in Acanthiza reguloides; 3.4 (3-4) in Malurus cyaneus; 3.2 (2-4) in A. chrysorrhoa; 3.1 (2-4) in Rhipidura leucophrys* and Petroica phoenicea*; 3.0 (2-4) in Colluricincla harmonica*; and 2.6 in Smicrornis brevirostris (from Ford 1963, Rowley 1965, Courtney and Marchant 1971, Marchant 1974). Species asterisked above have cupular nests.

5.7 INCUBATIONAL BEHAVIOUR

Warblers began incubation soon after laying the last egg, as do most species of birds (Moreau 1946). In every case where at least one of the pair was marked, the presumed female, and never the male, incubated. The female incubates alone in Petroica, but both sexes incubate in many other native passerines (Appendix 1). When the female is the chief incubator the male usually feeds her (Welty 1975), and this is so in several native Muscicapidae. However, I never saw an adult grey warbler feeding another.

Davis (1954) showed that simple records of the presence or absence of females on nests, such as obtained by daily visits to several nests at various times of day, could be combined to give a figure for the

proportion of time spent incubating, as accurate as one derived from long hours of direct observation. During my daily rounds (at 10:00-15:00h) I carefully approached nests 342 times to determine whether a female was on or off. The results (Table 5.6) indicate that female grey warblers on average spent 68% of their time (60-72%) incubating, with the suggestion that time on the nest declined during the first four-fifths of the incubation period, and then rose slightly. Among birds where only one parent incubates, the proportion of time spent on the nest is usually 60-80% (Welty 1975). At Kowhai Bush female robins spent 81% of their time incubating (R. Powlesland, pers. comm.). This figure may be higher than for warblers because the male robin feeds the female.

Table 5.6 - Proportion of time spent incubating computed indirectly.

	day of incubation*					
	1-4	5-8	9-12	13-16	17-20	overall
no. times ♀ on	65	48	41	41	38	233
total records	90	67	61	68	56	342
% times ♀ on	72.2	71.6	67.2	60.3	67.9	68.1

* day 1 = day last egg laid

5.8 INCUBATION PERIOD

The incubation period of passerines is taken as the interval in days between laying and hatching of the last egg in the clutch (day of laying = day 1), unless incubation starts before clutch-completion (Moreau 1946). Instead of calculating to the nearest whole day, I corrected the intervals for each egg as follows:

a. Since eggs were laid close to sunrise (section 5.3), their first calendar day in the nest was only about 0.8 days, and I subtracted 0.2 days from each interval.

b. I examined nests once daily close to noon, but eggs may have hatched at any time, so the appearance of a nestling indicated up to 0.5 days' incubation for the egg that day. Therefore, I subtracted the complement (0.5 days) from each interval.

c. From the nestling's weight I judged how recently the egg hatched and subtracted a fraction of a day (see Table 6.2) from the incubation period. A nestling of ⩾ 1.5 g probably hatched on the previous day after my inspection.

An underlying assumption in this analysis was that eggs hatched in the order laid (see section 6.1).

The average incubation period of grey warblers (time in the nest of the fourth egg; Table 5.7) was 19.5 days (range = 17-21 days). The 2-day laying-interval (section 5.4) caused early eggs to be in the nest for up to nearly seven days longer, and first eggs persisted for 24 days on average.

Passerines which nest in holes or have enclosed nests, tend to have longer incubation periods than those with cupular nests (Lack 1948). The New Zealand passerines studied to date follow this trend; incubation periods are longer in *Acanthisitta chloris* and in the grey warbler, than in the birds with cupular nests (Appendix 1).

Table 5.7 - Average times in the nest (days) of eggs in clutches of four. The value for egg-4 is the incubation period.

	egg				
	1	2	3	4	all eggs
$\bar{x}$	24.0	22.2	20.6	19.5	21.6
n	14	17	16	14	61
s	1.38	1.15	1.03	1.25	2.04
minimum	22.3	20.9	19.3	17.3	17.3
maximum	26.3	24.3	22.3	21.3	26.3

Details of incubation in passerines of temperate Australia are few (Courtney and Marchant 1971). The incubation periods of Acanthiza chrysorrhoa (18-20 days; Ford 1963) and Smicrornis brevirostris (19-20 days; Courtney and Marchant 1971) are as long as the grey warbler's, while those of Malurus cyaneus ($\bar{x}$ = 13.5 days, range = 13-15 days; Rowley 1965) and Rhipidura leucophrys (14 days; Marchant 1974) are much shorter. Australian Gerygone are said to incubate for only 12-14 days (Schodde in Frith 1976).

5.9 DELAY BETWEEN CLUTCHES

In two cases, warblers started repeated clutches in new nests 10 and 12 days after first clutches were abandoned. In four other instances known less exactly, the interval between desertion of the first nest and re-laying was 22-88 days, but fruitless attempts at re-nesting may have passed undetected. Fernbirds laid replacement clutches 5-43 days after deserting first clutches (Best 1973).

Intervals between fledging of a first brood and initiation of a second clutch were: 14 days (one fledgling); 15, 15 and 20 days (two fledglings); 42 days (three fledglings); and 20 and 35 days (four fledglings). This compares with a week to a month in *Acanthiza chrysorrhoa* (Australia; Ford 1963)

6. NESTLINGS

6.1 HATCHING

I marked some eggs in three clutches, and the limited data suggested that hatching was in the order of laying. A last (fourth) egg laid was last to hatch, a third egg hatched last when the fourth was removed by a cuckoo, and a first egg laid did not hatch last. In *Parus major* the first five eggs of a clutch (7-15 eggs) hatch in no set order, but those remaining nearly invariably hatch in the order laid, and the last egg laid hatches last (Gibb 1950). Eggs of the fernbird hatch in the order laid (Best 1973).

I visited nests daily (10:00-15:00h) during hatching, and assumed that a nestling seen on day 2 but not on day 1 hatched on day 2 unless its initial weight was 1.5 g or more (hatching the previous day likely). Eggs in clutches of four rarely all hatched together, and hatching of the clutch during two or three days was about equally common (Table 6.1), as far as once-daily inspection revealed. The modal pattern (35%) was for three eggs to hatch on day 1 and the fourth on day 2.

Table 6.1 - Pattern of hatching determined by once-daily inspection (clutches of four).

eggs hatched				
day 1	day 2	day 3	frequency	
1,2,3,4			2	
1,2,3	4		7	
1,2	3,4		2	11
1	2,3,4		2	
1,2,3		4	1	
1,2	3	4	3	7
1	2,3	4	2	
1	2	3,4	1	
			n = 20	

To determine more accurately the spread of hatching I used initial weights of nestlings to estimate their age (Table 6.2), interpolated from the observations that newly-hatched young were less than 1.0 g (Appendix 3), and that nestlings on their second day (age 1) weighed 1.54 g on average (Table 6.5).

Table 6.2 - Estimated age-weight relationships of nestlings on their day of hatching.

weight (g)	estimated age (days)
< 1.0	0
1.0	0.1
1.1	0.2
1.2	0.3
1.3	0.4
1.4	0.5
1.5	0.7
1.6	0.8
> 1.6	1

The average spread of hatching (difference in age between nestlings 1 and 4; Table 6.3) was 1.4 days (range = 0.3-2.1 days). Hatching intervals in fernbirds are 0.3-1.0 days (clutches of 2-3; Best 1973).

Table 6.3 - Difference in age (days; estimated from initial weight) of pairs of nestlings numbered in the order of hatching (broods of four).

	pair of nestlings			
	1+2	2+3	3+4	1+4
$\bar{x}$	0.20	0.40	0.84	1.42
n	14	14	13	13
s	0.33	0.36	0.54	0.50
range				0.3 - 2.1

Female warblers do not incubate until the clutch is complete (section 5.7), yet the average difference in age between nestlings paired in the order of hatching increases successively and geometrically (Table 6.3). This suggests that early eggs developed before incubation began properly. The 2-day laying-interval (section 5.4), such that the first egg is six days older than the fourth, doubles the exposure to ambient heat that would otherwise be experienced.

6.2 DATES OF HATCHING AND FLEDGING

Figs 6.1 and 6.2 give dates of hatching and fledging of individual nestlings, with data for 1976/77 and 1977/78 separate. The data for the two seasons are combined in Fig. 8.1. Where I did not know these dates exactly I estimated them from known dates of laying, hatching or fledging and the average incubation and nestling periods. I combined observed and estimated dates in Figs 6.1 and 6.2, but distinguished hypothetical dates of hatching and fledging calculated for eggs which failed to hatch and young which did not fledge for natural reasons.

Warblers at Kowhai Bush hatched during 14-16 weeks, from mid-September (earliest hatching 20.ix.1977) to early January (latest hatching 3-8.i.1977), in two bouts corresponding with early and late clutches. Warblers fledged during the same number of weeks and with the same bimodality, from early October (earliest fledging 8. x.1977) to mid-January (latest fledging 20-25.i.1977). The earliest that a late nestling hatched and fledged was 15.xi.1977 and 2.xii.1977 respectively. Breeding was slightly earlier in 1977 than in 1976 (see section 5.2).

Fifty-five cards of the Nest Record Scheme for warblers throughout New Zealand showed hatching in every week from early September to the third quarter of December, and fledging in every week from the third quarter of September to that of January. A few exceptional cards gave dates before and after these periods, but otherwise the data from Kowhai Bush seem typical of those for the country in general. There are

Figure 6.1 - Dates of hatching of warblers at Kowhai Bush, grouped into weeks.

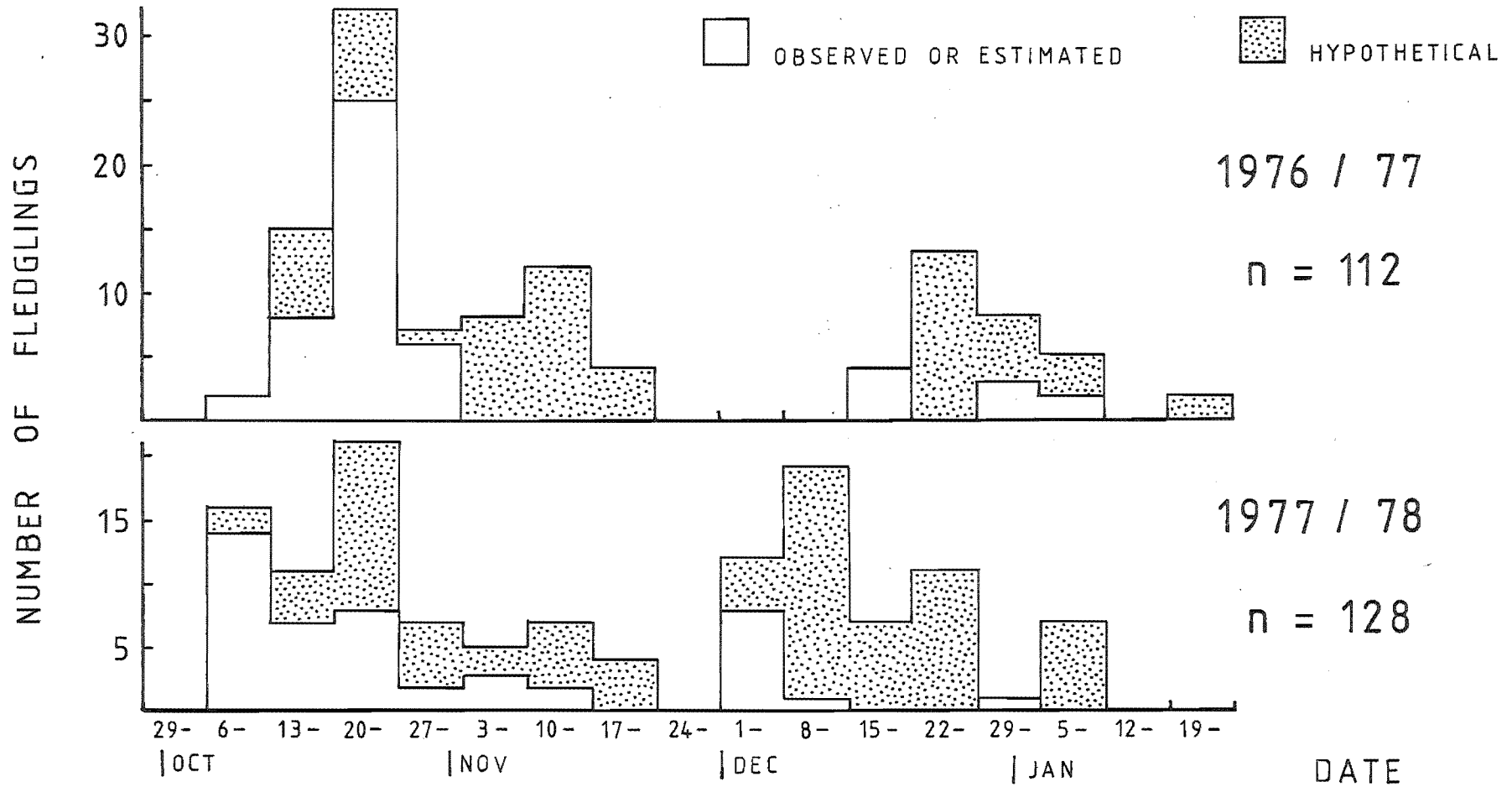

Figure 6.2 - Dates of fledging of warblers at Kowhai Bush, grouped into weeks.

records in the Classified Summarised Notes ("Notornis" 1(7): 79) of nestlings in late July and fledglings in May.

6.3 BROOD-SIZE

The average numbers of warblers to hatch and fledge per unparasitised nest (Table 6.4) show that fewer nestlings fledged per nest than hatched (see section 8.2 for causes of mortality). On average late nests had fewer young than early nests. Late clutches were smaller on average than early ones by only 0.11 eggs (Table 5.4), but late nests had 0.42 hatchlings and 0.91 fledglings fewer. Thus mortality increased during the breeding-cycle, but more severely for late nests than for early ones.

Table 6.4 - Numbers of warblers hatched and fledged per unparasitised nest (data for 1976/77 and 1977/78 combined).

	nestlings hatched			nestlings fledged		
	$\bar{x}$	n	s	$\bar{x}$	n	s
early nests	3.00	28	1.59	2.04	29	1.74
late nests	2.58	12	1.93	1.13	15	1.81
all nests	2.88	40	1.68	1.73	44	1.80

There was no appreciable difference between two years in the average number of young to fledge per nest (1.74 in 1976/77; 1.71 in 1977/78), but whereas 3.3 nestlings hatched on average per nest in 1976/77 only 2.4 did in 1977/78, and the discrepancy was greatest for early nests (3.6 cf. 2.4). This implies greater mortality of eggs in 1977/78, but greater mortality of nestlings in 1976/77 (see section 8.2).

6.4 NESTLING PERIOD

I calculated the time in the nest of each nestling as the difference between the day of hatching (day 0) and the day of fledging (the day on which once-daily inspection first showed the nestling to have fledged), with the following refinements:

a. I added to each interval the fraction of a day which represented the nestling's age (estimated from weight) at its first examination (see Table 6.2).

b. I subtracted 0.5 days from each interval, since I assumed that on average nestlings fledged mid-way between the visit on which they were last seen and that on which they were first absent.

The average nestling period of individual warblers was 17.2 days (n = 52, s = 0.86, range = 15.0-18.5).

Nestling period is said to be related to the nest's safety from predation, species with enclosed nests tending to have longer nestling periods than open-nesters (Lack 1948). Native New Zealand passerines, however, do not follow this trend, though they conform to the analagous one for incubation period (section 5.8). The grey warbler's nestling period is not, as expected from nest-type, second longest of those species studied (Appendix 1), after that of the hole-nesting Acanthisitta, though it is longer than for Rhipidura or Zosterops.

As with incubation period, the warbler's nestling period is similar to that of Acanthiza chrysorrhoa in Australia (17-19 days; Ford 1963) but greater than for Malurus cyaneus (12-14 days; Rowley 1965), for Rhipidura leucophrys (14 days; Marchant 1974) and than alleged for Australian Gerygone (10-12 days; Schodde in Frith 1976).

Since warbler-eggs are so large (section 5.5), hatchlings should be relatively more advanced than in species with normal-sized eggs, and this appears to be so. On day 0 warblers were 1.2 g on average or 16% of their maximum average nestling-weight (7.4 g; Table 6.5). This compares with 13% for the white-crowned sparrow (*Zonotrichia leucophrys*, Emberizidae; from Banks 1959), 11% for the cactus wren (*Campylorhynchus brunneicapillus*, Troglodytidae; from Anderson and Anderson 1961) and 10% for the English robin (*Erithacus rubecula*, Turdidae; from Lack and Silva 1949). On day 0 warblers were 18.6% of the average adult weight (6.4 g), compared with 6-8% for most passerines (Nice 1943 = 1964), 9.6% in cactus wrens and 13.1% in rufous-winged sparrows (*Aimophila carpalis*, Fringillidae; Austin and Ricklefs 1977).

6.5 GROWTH: WEIGHT

To quantify the growth of nestlings I weighed warblers (to the nearest 0.1 g) once daily (between 10:00 and 15:00h) during the first two summers. Unless otherwise stated, data are for 1976/77 and 1977/78 combined. Day 0 was that on which daily visits first revealed the nestling, that individual thus being less than 24 hours old. As with Banks (1959) I did not induce defecation if faecal sacs were visible in the cloaca, nor did I correct for defecation before weighing. Because weight was affected by how recently the nestling defecated and ingested, I also took linear measurements (section 6.6), although the errors inherent in weights are mostly overcome by the large samples described here. I excluded from the analysis data for 14 nestlings which lost weight and died.

The average weights of all healthy nestlings for each day of the nestling period (Table 6.5; data plotted on Fig. 11.4) allow approximate ageing up to day 12 since the means are well separated from each other. However, as Banks (1959) and Anderson and Anderson (1961) found, the range of weights for a day overlaps with at least the next mean in either direction.

Growth-curves of weight for nestling passerines are mostly sigmoid (by definition they approach an asymptote) and are probably best fitted by the logistic equation (Ricklefs 1967, 1968a). However, grey warblers have non-sigmoid average curves of weight (Fig. 6.3) whereby the maximum is reached on day 13-14, and there is a recession in weight before fledging. This pattern of growth is restricted primarily to oceanic birds and to the swallows and swifts (Ricklefs 1968b), and its occurrence in a small song-bird which gleans insects from foliage is unexpected. Taylor and Roberts (1962) described a similar weight-curve for the growth of Adélie penguin-chicks. The data more closely fitted a truncated normal curve than a Gompertz or logistic curve.

Nestlings fledged at various ages so I considered the weight of each, irrespective of age, on the last day in the nest. Comparisons of the average maximum weights (days 13 and 14 combined) with the average final weights on the day before fledging (Table 6.6), show statistically significant recessions in weight for all nestlings combined and for those in broods of four. The average recession (maximum weight minus final weight) was 0.31 g (all nestlings) or 4.2% of the maximum nestling-weight. This is a relatively small recession - corresponding figures

Table 6.5 - Weights (g) and linear measurements (mm) of nestling grey warblers; day 0 = day of hatching.

age	weight				tarsus				culmen			
	$\bar{x}$	n	s	range	$\bar{x}$	n	s	range	$\bar{x}$	n	s	range
0	1.18	57	0.16	0.9-1.6	6.77	57	0.41	5.8-7.6	4.91	35	0.18	4.6-5.2
1	1.54	63	0.21	1.2-2.1	7.49	61	0.51	6.5-8.7	5.27	37	0.24	4.8-5.6
2	2.05	66	0.29	1.3-2.8	8.63	66	0.59	7.6-10.0	5.92	39	0.29	5.4-6.7
3	2.69	59	0.34	1.9-3.5	9.92	58	0.77	8.4-11.6	6.59	39	0.28	5.9-7.2
4	3.33	64	0.39	2.0-4.0	11.39	64	0.91	9.0-13.0	7.23	37	0.28	6.6-7.9
5	4.04	57	0.45	2.4-4.7	12.93	46	0.97	10.0-14.3	7.74	33	0.26	7.2-8.3
6	4.74	52	0.46	3.6-6.0	14.34	52	0.97	12.0-16.2	8.20	33	0.27	7.8-8.8
7	5.43	56	0.53	4.0-6.3	15.71	56	1.07	12.6-17.4	8.60	30	0.25	8.2-9.1
8	6.03	59	0.49	4.6-7.0	16.99	59	0.97	14.0-18.8	8.99	26	0.26	8.5-9.5
9	6.48	60	0.59	5.1-7.5	18.39	60	0.97	15.4-20.1	9.32	33	0.28	8.8-10.0
10	6.85	52	0.52	5.7-8.0	19.47	52	0.97	17.2-21.4	9.65	26	0.28	9.2-10.3
11	7.16	48	0.57	6.0-8.4	20.35	47	0.86	18.1-21.6	9.97	22	0.28	9.5-10.7
12	7.30	47	0.55	6.1-8.6	21.03	47	0.82	19.3-22.4	10.22	24	0.26	9.7-10.9
13	7.36	51	0.54	6.3-8.7	21.44	50	0.85	19.3-22.7	10.44	22	0.28	9.9-11.1
14	7.35	48	0.47	6.6-8.8	21.76	48	0.81	20.0-23.5	10.65	24	0.32	10.0-11.4
15	7.20	47	0.49	6.5-8.9	21.87	46	0.82	20.0-23.6	10.82	25	0.41	10.1-11.6
16	7.09	45	0.53	6.0-8.4	21.87	44	0.79	20.3-23.3	11.02	18	0.30	10.3-11.6
17	7.02	20	0.64	6.0-8.1	22.04	17	0.67	20.9-23.6	11.40	8	0.30	11.0-11.9

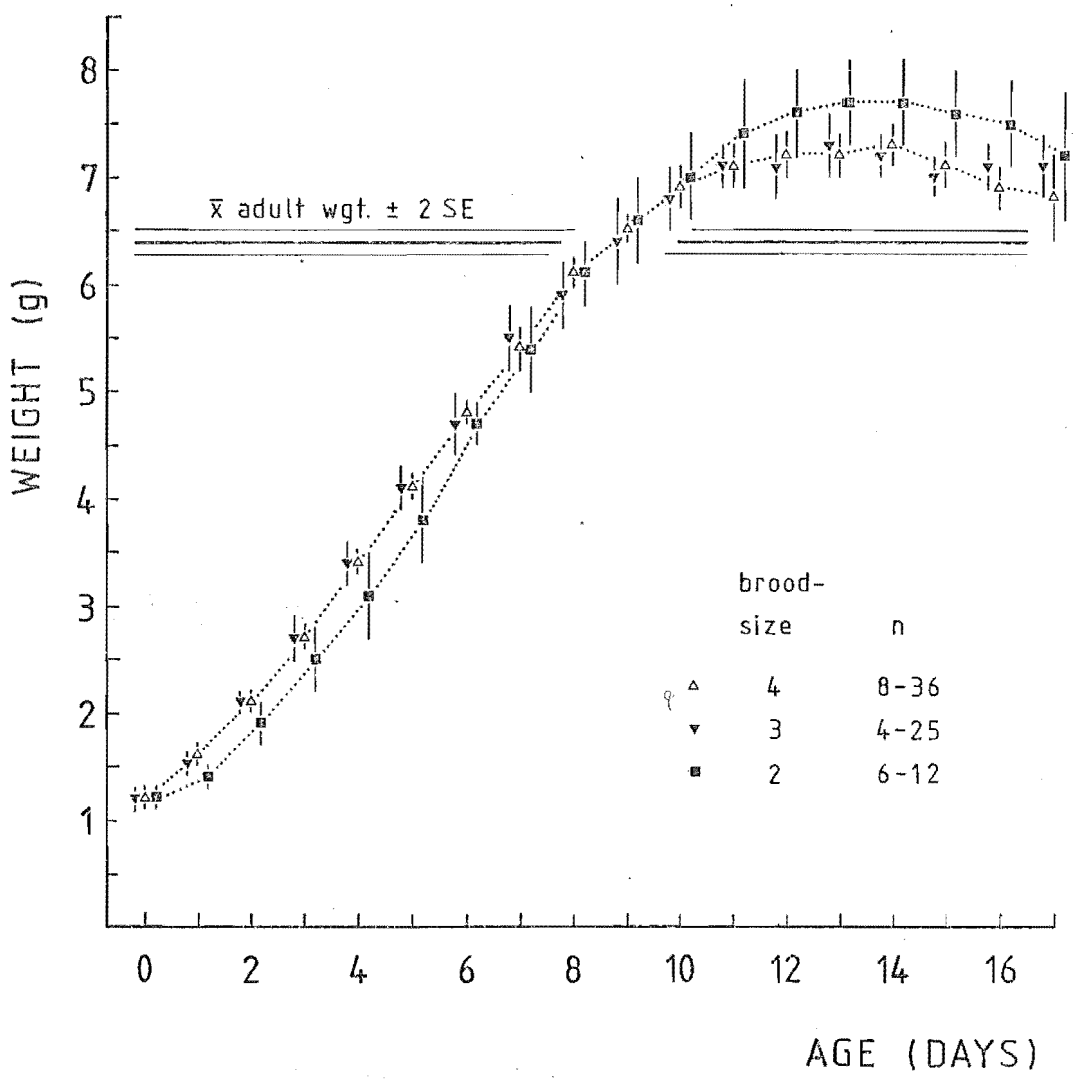

Figure 6.3 - Average weight-age-curves for nestling warblers in broods of two, three and four; mean ± 2 SE (points offset horizontally for clarity).

for house martins (Delichon urbica), house sparrows (Passer domesticus) and blue tits (Parus caeruleus) are 27.2%, 10.4% and 4.4% respectively (O'Connor 1977).

Table 6.6 - Maximum and final weights (g) of nestlings in broods of different size (maximum - age 13+14; final - day before fledging).

	maximum			final			t-test		
brood-size	$\bar{x}$	n	s	$\bar{x}$	n	s	t	d.f.	P
4	7.24	45	0.39	6.86	25	0.45	3.59	44	<0.002
3	7.25	30	0.47	7.06	19	0.39	1.48	43	NS (P>0.1)
2	7.69	24	0.61	7.53	8	0.41	0.88	18	NS (P>0.2)
all	7.35	99	0.51	7.04	52	0.48	3.80	149	<0.001

Ricklefs (1968b) and O'Connor (1977) showed (respectively) that barn swallows (Hirundo rustica) and house martins receded in weight before fledging entirely by loss of water, mostly from the integument. To test the hypothesis that the recession in weight of nestling warblers is due to loss of water I analysed the composition of 26 nestlings of known age, and five full-term embryos removed from their eggs. The sample-size was small so I grouped nestlings into five age-categories. The results (Fig. 6.4) show that water, lipid and other constituents (bone, feathers, protein etc.) tended to increase in absolute amount as the nestlings grew. The amount of water, however, declined towards the end of the nestling period, suggesting that the recession in weight was due to loss of water.

The mean weight of adult warblers was 6.4 g. Thus in Fig. 6.3, which shows the average weights of nestlings in broods of two, three and four, all curves exceed the mean adult weight - another extremely unusual phenomenon in song-birds. Every healthy nestling (n = 71) exceeded the mean adult weight during its development, the heaviest (8.9 g on day 15) being 39% heavier than the average adult. Nestlings on their last day in the nest were also heavier than the average adult, irrespective of brood-size (Table 6.6), and on average they fledged at 110% of the mean adult weight. No data are available for other Gerygone or related species.

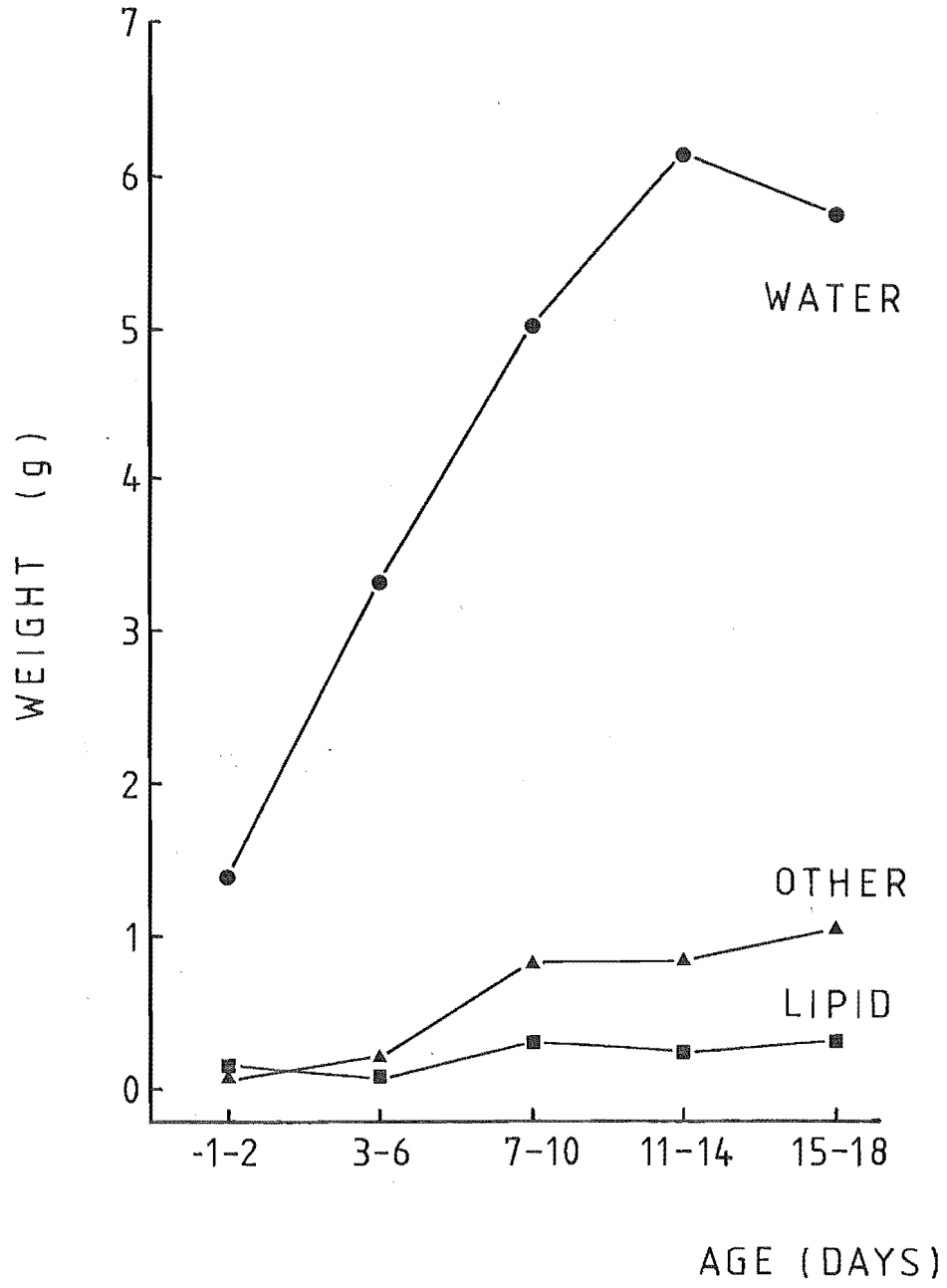

Figure 6.4 - Quantity of water, lipid and other constituents in nestling warblers, as a function of age; n = 9, 3, 8, 8 and 3 for the respective age-groups.

In species with sigmoid growth, the asymptote of the growth-curve is an important parameter. Since grey warblers have non-sigmoid growth with maximum weight reached at 13-14 days on average, I equated asymptote with maximum weight. Individuals reached maximum weight (6.7-8.9 g) as early as 10 days old or as late as 17. For 30 nestlings weighed daily during this period I calculated the ratio R (growth-curve-asymptote : mean-adult-weight; Ricklefs 1968a), for which the range was 1.05-1.39 ($\bar{x}$ = 1.18, n = 30, s = 0.08). R exceeds one in many oceanic birds, and in nestling swifts and swallows (which are fed on insects caught on the wing), but R is close to one for passerines which glean invertebrates from foliage and for "flycatchers" (Ricklefs 1968a).

The following analyses test the null hypothesis that on average nestlings from broods of two, three and four did not differ in their growth in weight. Fig. 6.3 shows average weight-age curves for broods of different size, and I analysed the curves statistically in three parts. Between the ages of 0 and 9 days (inclusive) linear regressions of weight on age fit well for nestlings in broods of four, three and two (Table 6.7 a-c). Slopes are similar but the y-intercept for broods of two is lower than for broods of three and four. Comparing the lines (broods of four vs. broods of three; broods of four vs. broods of two) for heterogeneity of variance, they are significantly different ($\chi^2 > 55$ for 1 d.f.; $P < 0.001$). This confirms the visual impression (Fig. 6.3) that for days 1-7 nestlings in broods of two were lighter on average than the others. The energy-requirement of single nestlings is inversely related to brood-size (Royama 1966), so nestlings of a pair possibly had a larger energy-requirement during the poikilothermic stage of development, and thus a lower average weight, than those in broods of three and four. Alternatively, parents of broods of two may be less efficient than those of larger broods.

Comparing the peaks of the growth-curves (average weights of nestlings aged 13 and 14 days; Table 6.6), there was a significant difference between broods of four and two (t = 3.30 for 33 d.f.; $P < 0.01$) and three and two (t = 2.96 for 43 d.f.; $P < 0.01$). Nestlings from broods of three and four were not significantly different (t-test; $P > 0.1$). Thus where only two nestlings were present they reached the highest maximum weights. Similarly, Gibb (1950) found that tits (*Parus*) from small broods were heavier on average than those from large. Nestlings in small broods may individually receive more feeds than those of larger broods (Royama 1966), and on average warblers in broods of three got

Table 6.7 - Linear regressions of weight and tarsal length on age for nestlings 0-9 and 3-9 days old respectively (1976/77 and 1977/78).

			WEIGHT			TARSUS		
	brood-size	n	r^2	regression eqn.	n	r^2	regression eqn.
years and	4	302	0.96	[a] $y = 0.62 x + 0.96$	213	0.94	[h] $y = 1.43 x + 5.79$
early/late broods	3	198	0.93	[b] $y = 0.61 x + 1.01$	128	0.86	[i] $y = 1.40 x + 5.84$
combined	2	93	0.94	[c] $y = 0.65 x + 0.74$	66	0.89	[j] $y = 1.43 x + 5.08$
years early broods	4	204	0.96	[d] $y = 0.62 x + 0.91$	136	0.94	[k] $y = 1.45 x + 5.39$
combined late broods	4	98	0.97	[e] $y = 0.61 x + 1.11$	77	0.97	[l] $y = 1.42 x + 6.39$
early broods 1976/77	4	96	0.96	[f] $y = 0.63 x + 0.99$	57	0.94	[m] $y = 1.43 x + 5.72$
early broods 1977/78	4	108	0.96	[g] $y = 0.63 x + 0.78$	79	0.97	[n] $y = 1.48 x + 5.01$

more visits per nestling than those in broods of four (section 12.6). If this pattern extends to nestlings in broods of two, then once homoiothermic, they may benefit to the extent of the weight-differences shown.

Linear regressions of weight on age between days 15 and 18 (inclusive) fit poorly (r^2 = 0.05, 0.01 and 0.05 for broods of two, three and four respectively), so I compared the average weights of nestlings on the day before fledging (Table 6.6). There was no significant difference between the final weight of nestlings in broods of four and three, but differences were significant when these were each compared with broods of two (respectively: $t = 3.93$ for 13 d.f., $P < 0.002$; $t = 2.73$ for 13 d.f., $P < 0.02$). Thus the final weights paralleled differences in the maximum weights for broods of different size.

I conclude that for the first half of the nestling period, nestlings from broods of two were lighter on average than those from larger broods. Thereafter nestlings from broods of two achieved higher maximum and final weights than the others.

Since I found fewer late than early nests, and the survival of late nestlings was poor, the data were sufficient for comparison of early and late nestlings only from 0-9 days old in broods of four. Linear regressions of weight on age (Table 6.7 d,e) fit well. Slopes are similar, but the variances are significantly heterogeneous (χ^2 = 68 for 1 d.f.; $P < 0.001$) and the y-intercepts differ suggesting consistently lower weight during this part of the nestling period for nestlings in early broods. Perhaps the food-supply was greater or more suitable for nestlings later in the season (see section 8.2).

Comparison between the two years was best served by the data for early broods of four. Linear regressions of weight on age for nestlings 0-9 days old (Table 6.7 f,g) fit well, have identical slopes but different y-intercepts. The variances are significantly heterogeneous (χ^2 = 52 for 1 d.f.; $P < 0.001$). Nestlings during this stage were apparently heavier in 1976/77 than in 1977/78, suggesting that conditions were worse for warblers in the second summer. However, nestlings of 13 and 14 days old (early broods of four) had the same average weight in both years (7.23 g in 1976/77; 7.25 g in 1977/78).

6.6 GROWTH : LINEAR MEASUREMENTS

Once daily, as far as possible, I measured (to the nearest 0.1 mm) the tarsus (actually tarso-metatarsus) and total culmen of nestlings. Right tarsus, measured in 1976/77 and 1977/78 was taken diagonally from behind the tibio-tarsal joint to the anterior flexure of the folded foot. Total culmen, measured only in 1976/77, was on the right side, from the posterior tip of the rictal flange to the tip of the bill. Criteria for excluding unhealthy nestlings from the analysis, and for defining day 0, were as for section 6.5. Unless otherwise stated I pooled data for tarsus from both years.

The average tarsal lengths for all healthy nestlings (Table 6.5) are useful as a guide to ageing, especially in association with weights. These data when plotted (Fig. 6.5) yield an apparently sigmoid curve. The curve appears linear between the ages of 3 and 9 days (inclusive), so for these data I obtained linear regressions of length on age (Table 6.7 h-n) to compare the effects of brood-size, stage of the breeding-season, and year. All equations fit well and have similar slopes, though y-intercepts differ. However, comparing the lines (broods of four vs. broods of three; broods of four vs. broods of two; early vs. late; 1976/77 vs. 1977/78) variances are not significantly heterogeneous (χ^2-test; $P > 0.1$) and analyses of covariance show that slopes and intercepts do not differ significantly (F-test; $P \geqslant 0.05$).

Tarsal lengths before fledging, of nestlings in broods of four, three and two, were respectively 21.93 mm (n = 23, s = 0.89), 21.96 mm (n = 16, s = 0.79) and 22.39 mm (n = 8, s = 0.68). There was no significant difference (t-test; $P > 0.1$) between broods of four and two.

The average lengths of total culmen (Table 6.5) are useful for ageing nestlings, especially young ones, in association with weight and tarsal length. The average growth-curve for total culmen (Fig. 6.5) is apparently non-sigmoid, perhaps because the parameter is a complex one - elongation of the bill being accompanied by shrinkage of the rictal flanges. Tarsal length, which undergoes greater absolute growth, is a more useful measurement than total culmen, particularly since the latter has no direct counterpart in the adult bird.

In 1976/77 the average wing-length (minimum chord of flattened but unstraightened right wing, from carpal joint to tip of longest primary remex; measured to nearest 0.5 mm) of 25 nestlings on the day before fledging was 40.0 mm (s = 2.31). The corresponding value (measured to nearest 1 mm) for 60 free-flying warblers was 52.8 mm

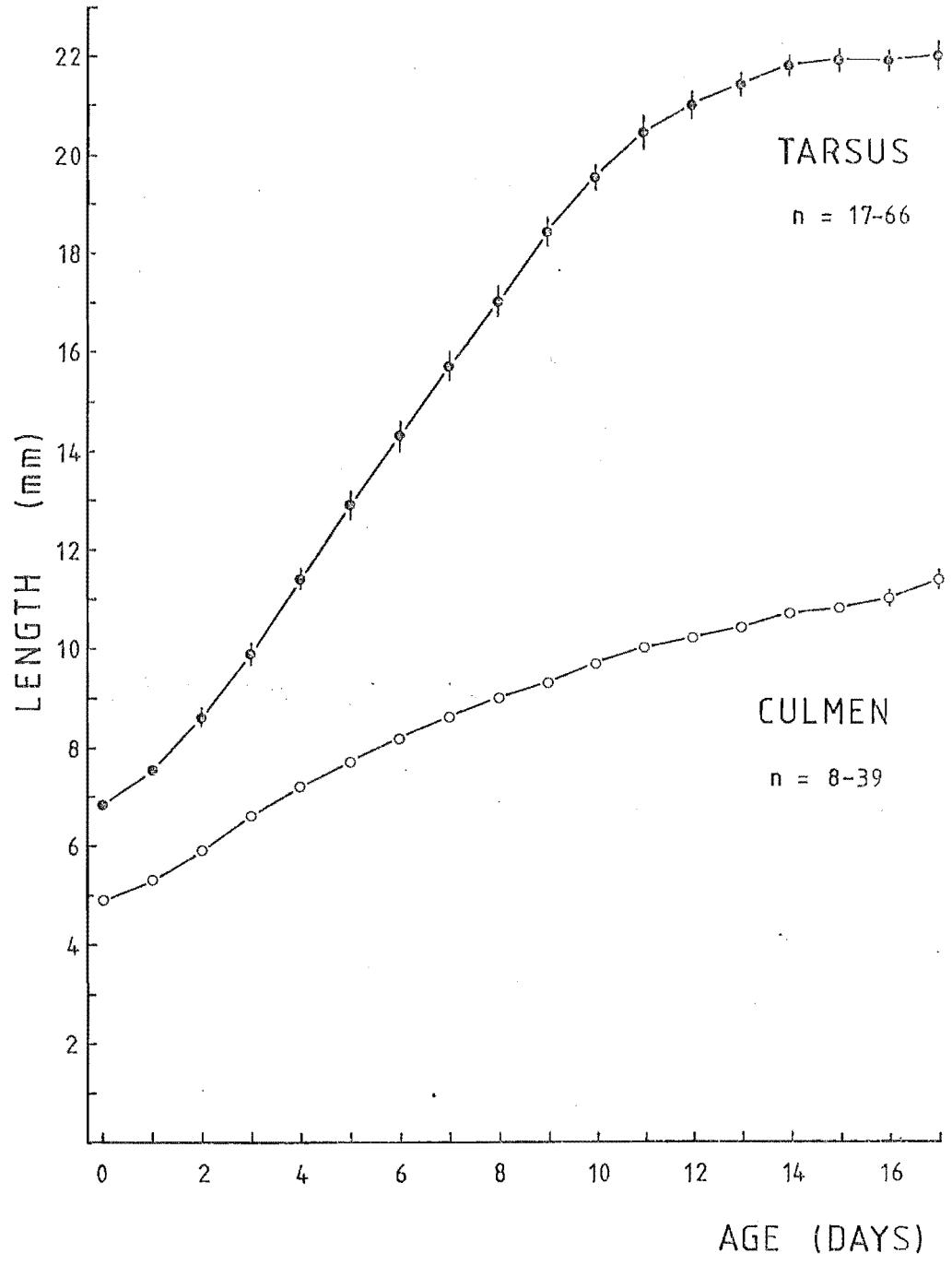

Figure 6.5 - Average length-age-curves for tarsus and culmen of nestling warblers; mean ± 2 SE (where 2 SE > 0.1 mm); see Table 6.5.

(s = 1.99), so grey warblers fledged with wings 76% as long as those of adults. For fernbirds the figure was 77-89% (Best 1973). The mean tarsal length (22.02 mm, s = 0.82) of 47 nestlings on the day prior to fledging did not differ significantly (t-test; $P > 0.2$) from the value for 20 free-flying birds (21.97 mm, s = 0.85), so the full length of this bone is attained in the nest. Even in *Aimophila carpalis*, with a nestling period of only 8-9 days, the tarsus reaches adult size at fledging (Austin and Ricklefs 1977).

6.7 STOMACH-CONTENTS OF NESTLING WARBLERS

To investigate the kind of food that warblers brought to their young, I removed the stomachs from 19 nestlings which died of natural causes. All were 10 days or older, collected from October to January. I examined the contents of the gizzard and proventriculus (though the latter was usually empty) under a dissecting microscope, and identified items of food to order. I measured or estimated the length of the longest axis of items to the nearest whole millimetre.

Grey warblers fed their nestlings solely on invertebrates; *Leptospermum* leaves and small pieces of grass which I found in some stomachs were probably ingested accidentally. Table 6.8 shows that the maximum number of items held in a single stomach was 31. On average there were 9.1 invertebrates per stomach, but several held only finely comminuted remains, suggesting that the nestlings were starved.

The proportion of stomachs in which a category of food appears indicates either selectivity or the availability of food. All stomachs contained insects and most held caterpillars. Dipteran flies and spiders were well represented.

Of all the items ingested by warblers, 45% were lepidopterans, 65% insects and 20% spiders. On average there were six insects (including four lepidopterans) per stomach and two spiders. Three stomachs contained small discoid snails 1-2 mm in diameter, suggesting that warblers will collect prey that is neither large nor fast-moving. Silvereyes in New Zealand also eat small snails (Kikkawa 1966). Nearly half the ingested items were 5 mm long or less (Fig. 6.6), even though the data refer to nestlings at least half-grown. In my sample, nearly all items longer than 10 mm were caterpillars. Similarly, nearly half the insects swallowed by nestlings of *Parus major*, and over 80% of those eaten by nestlings of *P. caeruleus* and *P. ater*, were less than 5 mm long (Betts 1955).

Table 6.8 - Classification by order of 173 invertebrates collected from 19 stomachs of nestling warblers.

	stomachs		total items		items/stomach	
	no.	%	no.	%	mean	maximum
Hemiptera	3	16	6	3.5	0.3	4
Coleoptera	9	47	9	5.2	0.5	1
caterpillars	17	90	72	41.6	3.8	16
moths	2	11	5	2.9	0.3	4
Lepidoptera	18	95	77	44.5	4.1	16
Diptera	12	63	21	12.1	1.1	3
INSECTA	19	100	113	65.3	6.0	21
Araneae ARACHNIDA	12	63	38	22.0	2.0	8
Unidentified arthropods	8	42	16	9.2	0.8	5
ARTHROPODA	19	100	167	96.5	8.8	31
Stylommatophora MOLLUSCA	3	16	6	3.5	0.3	3
INVERTEBRATES	19	100	173	100	9.1	31

6.8 BROODING AND SANITATION

Passerines are poikilothermic during the initial part of the nestling period and an adult regularly broods them until they develop homoiothermy, and during inclement weather (Welty 1975: 346). I did not see brooding of nestling warblers older than 10 days, so that all presumably maintained their body-temperature by that stage; some were seemingly not brooded after 5-6 days of age. Full grown nestling warblers were apparently never brooded, even during cold or wet weather, perhaps because of the advantages of the enclosed nest. Where the sexes of a pair were individually recognisable, always the female brooded, as in *Petroica* but in contrast to many other native passerines (Appendix 1). Both sexes of warbler fed the nestlings, a feature of all species listed in Appendix 1.

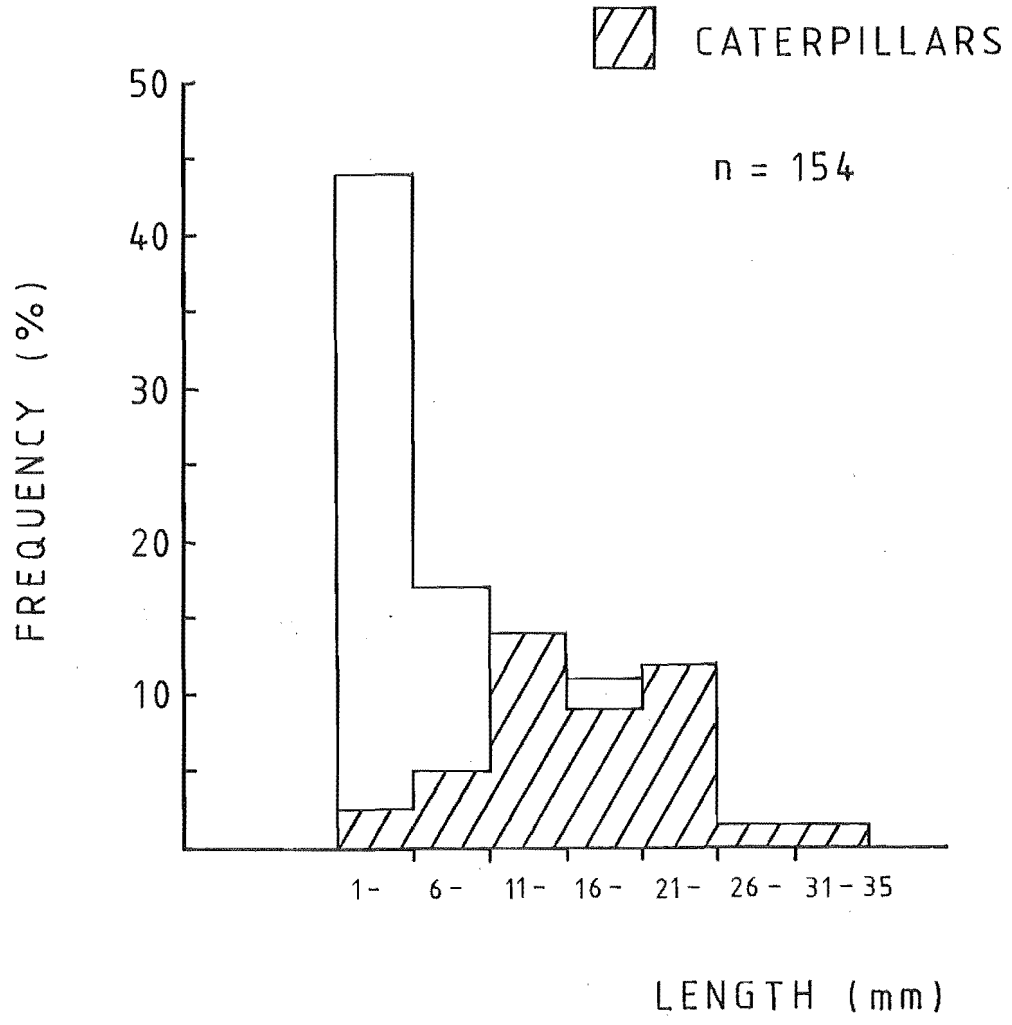

Figure 6.6 - Distribution of items from the stomachs of nestling warblers according to length of the longest axis.

In 1977/78 and 1978/79 (between 10:00 and 15:00h) I watched, in 60- or 30-minute spells for a total of 19 hours, the brooding of nestling warblers from broods of four or three (see section 11.5 for brooding of cuckoos). The proportion of time that the female devoted to brooding (Fig. 6.7) declined with maturation of the young, a result conforming with that of many similar studies of passerines (Welty 1975: 346). The linear regression of time spent brooding on day of brooding (day 1 = that on which the first nestling hatched and brooding commenced) fits well ($r^2 = 0.66$, $n = 23$) and is significantly linear (F-test; $P < 0.01$). The data are too few to determine satisfactorily whether the number of broodings per hour, or their duration, diminished concomitantly. According to the equation, time spent brooding fell to nil at 10.7 days, which supports observations above.

The rhythm of the male in bringing food to the nest was superimposed on the female's brooding-pattern rather inefficiently. Often the male arrived at the entrance just as the female had settled to brood. In this event the female always left, but sometimes reluctantly, and often she returned immediately the way was clear. Thus some brooding-spells lasted only a fraction of a minute (all treated as 0.5 minutes), while the longest was 30 minutes, although another, not timed to conclusion, lasted at least 38 minutes. The mean of 63 brooding-spells was 6.2 minutes but the variability was large ($s = 5.59$).

On 66% of occasions ($n = 67$) the female ceased brooding because the male arrived with food, and associated brooding-spells were 4.9 minutes on average ($n = 40$, $s = 4.73$). Otherwise she quitted the nest apparently spontaneously, or for an obvious reason such as to chase an intruder, and here brooding-spells were longer ($\bar{x} = 7.8$ minutes, $n = 21$, $s = 4.13$). The difference was significant ($t = 2.37$ for 59 d.f.; $P < 0.05$).

In typical passerine fashion adult warblers (of both sexes) removed faecal sacs from the nest if nestlings produced them immediately after ingestion. The enclosed nest precluded close observation, but clearly in many instances the adults prodded to stimulate defecation, and nestlings revolved in the nest and presented their rumps at the entrance. Adults carried the gelatinous faecal sacs to a perch at least 10 m from the nest, and I noticed that some were dropped. Adults at the nest sometimes made repeated swallowing motions, but whether they were eating faecal material or clearing their mandibles of the food they had just brought was unclear.

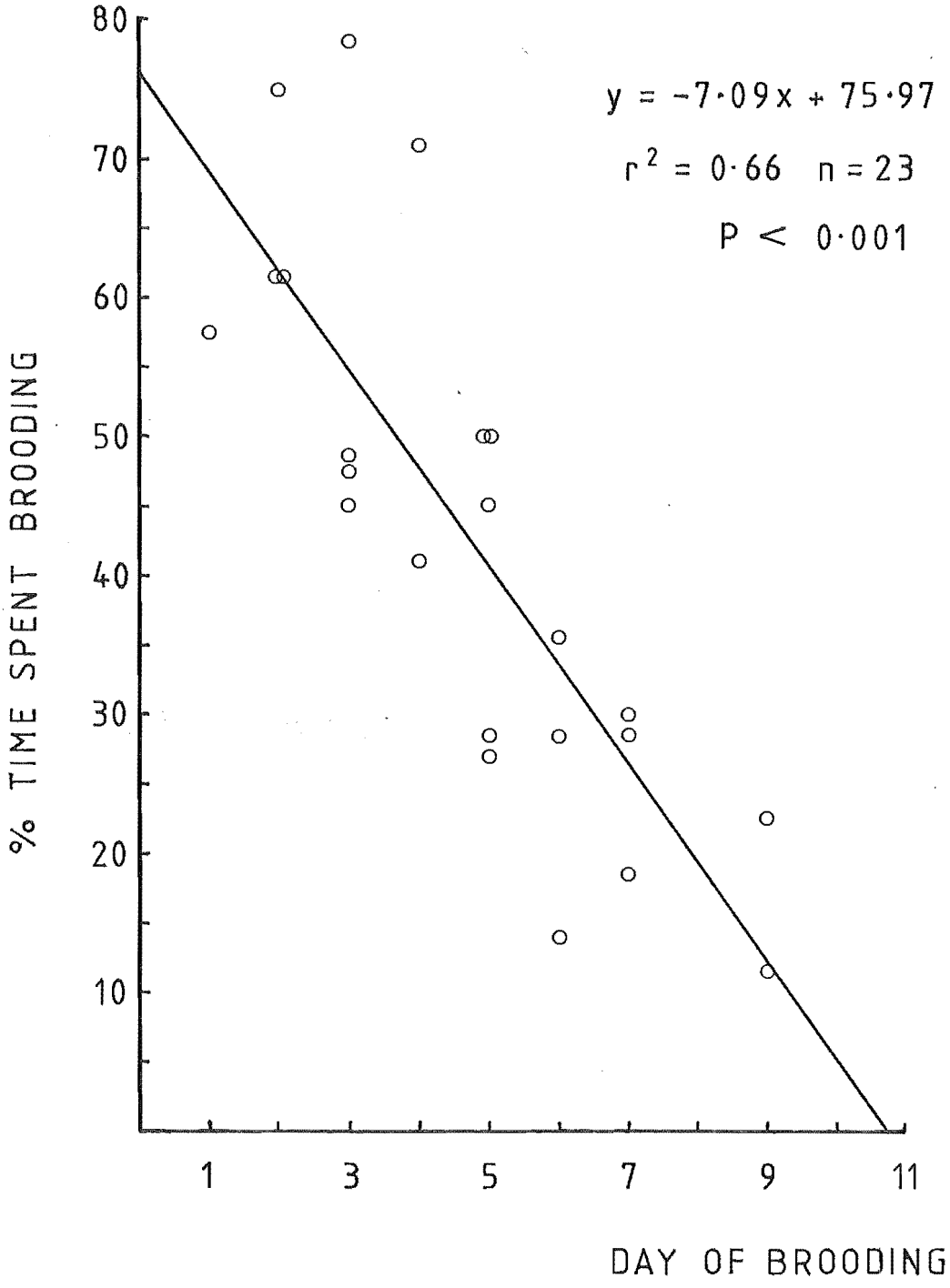

Figure 6.7 - Linear regression of time spent brooding on day of brooding, for nestling warblers.

Adults removed faecal sacs on about 30% of their visits to the nest (n = 376), with no apparent difference in this proportion between the sexes (♂♂ 32%, ♀♀ 29%). Nests were clean during the early stages, but as nestlings neared fledging, dried faecal sacs accumulated in the lining and mingled with the fragments of keratin derived from the developing teleoptiles. Many nests and nestlings at this stage became infested with mites.

7. JUVENILES

7.1 IDENTIFICATION

Young warblers were morphologically recognisable until about mid-March (two months after the last bird fledged). The irides were dark brown (red in adults), and the legs dull grey-pink (black in adults). The facial plumage was suffused with yellow, and a pale yellow circum-orbital ring was often apparent, even at a distance. The tail was noticeably short soon after the birds fledged, and, when fully-grown the tail was paler than in adults. The buccal lining, yellowish in fledglings, was black in adults.

Warblers became indistinguishable from adults apparently at their first moult, so there was no distinct immature plumage as occurs, for example, in males of *Malurus cyaneus* (Rowley 1965). Two banded warblers seemed to develop adult appearance in early February, 12 and 15 weeks after they fledged. At this time other banded juveniles had moulting tails and red irides. The moult of juveniles seemed to coincide with the post-nuptial moult of adults (January to March; section 8.1).

Strictly, a passerine is a juvenile only while wearing its first plumage of true feathers, and the assumption of adult plumage implies the attainment of sexual maturity (Thomson 1964). However, I applied the term "juvenile" to grey warblers between their day of fledging and the following August, the start of the breeding-season.

7.2 PARENTAL CARE

Warblers were fed for up to 35 days after fledging, though they caught some prey themselves from their 18th day out of the nest. They begged to their parents for up to 38 days. In general there were increasing signs of independence of the young about 30 days after fledging; begging declined,

parents were aggressive towards their young, and young began to stray from the group. Some juveniles were apparently independent at 28 days out of the nest.

Long periods of juvenile-dependency characterise native New Zealand passerines (Appendix 1), except *Zosterops lateralis*, which established in New Zealand from Australia during historical times. In Australia, fledglings of Acanthiza chrysorrhoa are dependent on parents for at least two weeks (Ford 1963); those of Malurus cyaneus for 30-40 days (Rowley 1965).

For 1-3 weeks after fledging, juvenile warblers of early broods usually stayed together and were fed by both parents, except that the male often dominated where only two young fledged. Then, during the next 1-3 weeks, the male often attended the juveniles alone, while the female left the group intermittently to build the second nest. When with the group at this time the female often ingested the food she collected and ignored, or drove off, juveniles which begged to her. In five cases 3-18 days elapsed between my last observation of a female feeding juveniles and the laying of her first egg in the new clutch. However, one of these females also joined her family and fed juveniles on the day after she laid a second egg (of four). Intervals of 14-42 days between fledging of a first brood and initiation of a second clutch (section 5.9), imply that many females spent little time assisting fledglings of an early brood.

The survival of young warblers during the period of dependency on parents was high. Of 48 banded warblers which fledged in the main study-area only two failed to survive the first nine days out of the nest. At least 39 (81%) survived for a minimum of 18 days after fledging, and at least 26 (54%) survived a minimum of 25 days. Ricklefs (1973) stressed the difficulty of determining post-fledging survival by direct observation, and he summarised the few available figures. In blackbirds (*Turdus merula*) 66% of fledglings survive 15-20 days out of the nest; 56% of ovenbirds (*Seiurus aurocapillus*) survive 30-35 days; 87% of cactus wrens (*Campylorhynchus brunneicapillus*) survive 21 days; 90% of black-capped chickadees (*Parus atricapillus*) survive 3-4 weeks; 62% of *Passer montanus* survive a month; and 22% of skylarks (*Alauda arvensis*) survive 25 days. Survival of dependent fledglings is high in most passerines, especially where the nestling period is long and the young thus fledge when physically advanced (Ricklefs 1973).

7.3 DISPERSAL

Of 44 nestlings banded in the main study-area (1976/77 and 1977/78), which fledged successfully, and survived for at least nine days out of the nest, I only saw 10 (23%) as independent birds. Likewise, of 22 nestlings banded beyond the main study-area (not all of which necessarily fledged) I only saw four (18%) as independents. Therefore, once free of their parents, most juvenile warblers either dispersed from their natal region, or died.

Fig. 7.1 and Table 7.1 give details of 22 point-to-point movements in the dispersal of 17 marked juveniles. I banded most as nestlings, but three I caught in mist-nets and recognised as juveniles from their appearance. The distance given is the shortest between the nest or net where I marked a bird and the location of its sighting. Where I saw a dispersing juvenile more than once I have given the distance from the new location to that of the previous sighting. I calculated time in a corresponding way, except for warblers banded as nestlings. These I assumed to be tied to the natal territory for 30 days after fledging, and I determined their dispersal from an estimated date of independence.

Two birds (1 and 2; Fig. 7.1, Table 7.1) dispersed through the main study-area after fledging from a nest at the opposite end of the bush. Three other birds (3,4,5) appeared at the other end of the forest after fledging in the main study-area. Several (7, 9,10,11,14 and 17) crossed from Habitat 2 to Habitat 1, although juvenile-10 went back again. Only one bird (16) moved from Habitats 1 to 2, but I found fewer nests in the former. The following pairs of re-sighted juveniles were siblings: 1+2, 3+6, 7+8, 9+10. The siblings apparently followed the same direction of dispersal (Fig. 7.1), though I saw them apart.

Obviously, juvenile warblers were highly mobile. All banded nestlings which I saw later as independent birds had moved at least 350 m from the nest in which they were raised. The furthest movement of a juvenile that I recorded was 2.9 km, and the average for all movements was 0.9 km (Table 7.1). Apart from the special case (12) where I once saw a bird 150 m from where I saw it 2½ hours before, the maximum average rate of travel was 52m/day. However, re-sightings of juveniles were almost entirely confined to the tracks which I frequented in the main study-area, and I did not search for birds in farmland and river-bed adjacent to the bush. Thus, because Kowhai Bush is long and thin in shape, I detected dispersal only along its length. In Britain great tits (Parus major) usually disperse 400-600 m (but up to 3.6 km) from their natal site to subsequent breeding-site (Greenwood et al. 1978).

Table 7.1 - Dispersal of juvenile warblers during their first calendar year. The numbers, corresponding with those of Fig. 7.1, refer to individuals. Multiple entries for an individual are for successive movements, the distances and times being calculated from the previous sighting.

no.	distance (m)	time (days)	average rate of travel (m/day)
1	1893	99	19
	404	180	2
2	2915	98	30
3	1204	76	16
4	2249	251	9
5	2851	251	11
6	511	17	30
7	1236	30	41
8	503	186	3
9	959	22	44
10	677	13	52
	372	28	13
11	808	27	30
12	384	59	7
	154	1	154
13	360	25	14
	178	26	7
	162	65	3
14	392	18	22
15	349	78	5
16	653	118	6
17	459	56	8
$\bar{x}$	894		23.8
			n = 22

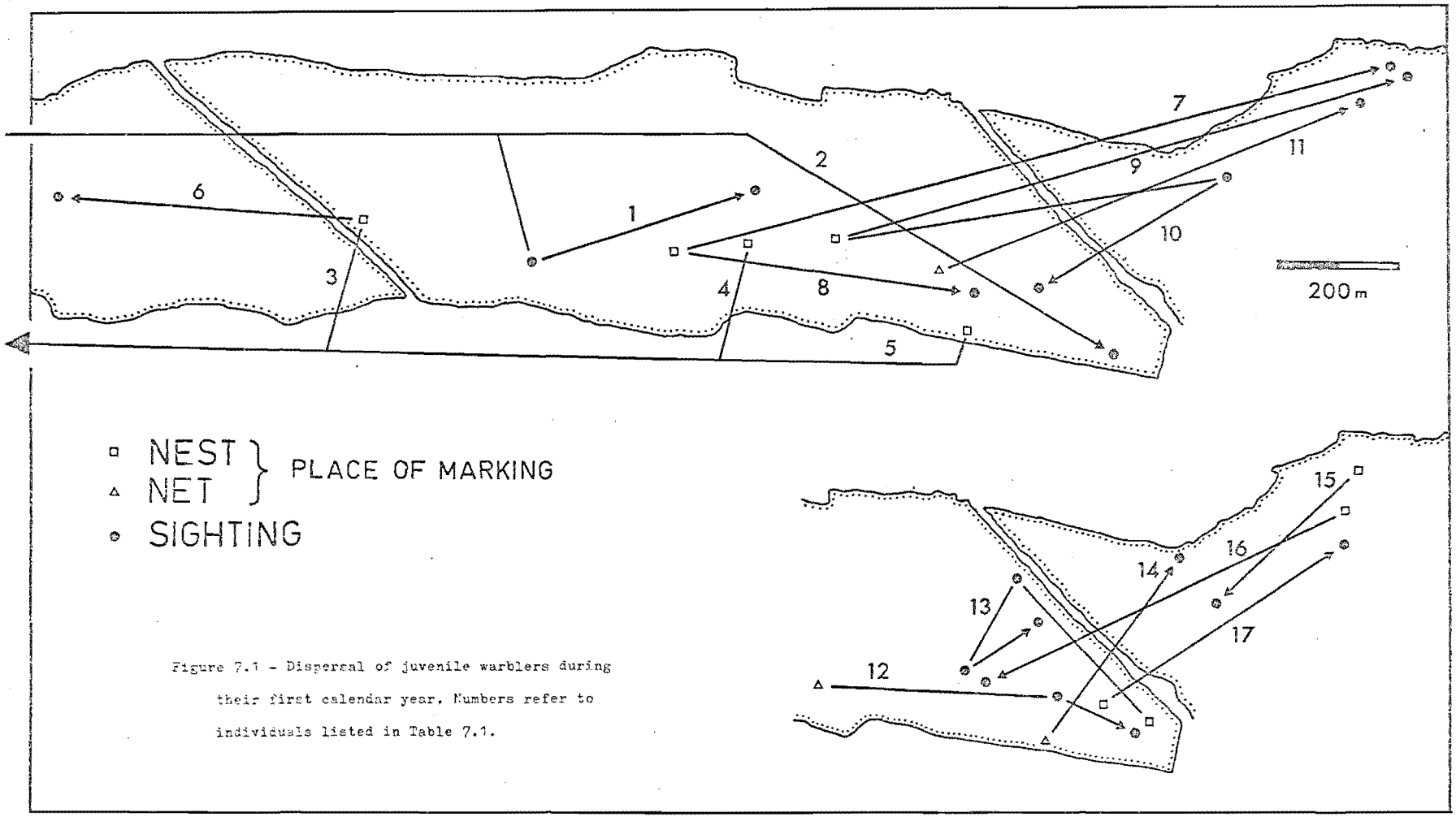

Figure 7.1 - Dispersal of juvenile warblers during their first calendar year. Numbers refer to individuals listed in Table 7.1.

In several Australian species, including close relatives of the grey warbler, young from a previous brood may cooperate with the adults in feeding a subsequent brood of nestlings (Ford 1963, Harrison 1969b). However, there was no evidence in this study that any warblers other than the true parents fed nestlings. In the Northern Temperate Zone families of some sedentary titmice may stay together during autumn and winter (Pettingill 1970), but banding of grey warblers yielded no evidence of this.

7.4 RECRUITMENT AND AGE AT FIRST BREEDING

The annual recruitment of juvenile warblers to the breeding population at Kowhai Bush was extremely small. In total I banded 89 nestlings during two breeding-seasons (1976/77 and 1977/78), and marked six apparent juveniles after netting them. Of these 95 birds, I knew of only six that later set up territories. Considering birds only in the main study-area, I banded 44 nestlings which fledged during the two summers, of which two (♂-L, ♂-M; 5%) joined the adult population. Yet the sample of 44 fledglings probably represented about 36% of the total production of the area. (Main study-area = 30 ha = 44 warbler-territories, since one territory = 0.68 ha; section 3.4. Two breeding-seasons = (a) 88 early nests, of which 62% or 55 would yield fledgling warblers; and (b) 88 late nests, of which 20% or 18 would yield fledglings (Table 8.1). Average nests yielded 1.7 fledglings - section 6.3 - so in two seasons the estimated 73 nests in the main study-area would have yielded about 124 young.) Thus, perhaps only three young are recruited in the main study-area per year.

Of the juveniles which joined the adult ranks, one was possibly a female. I saw it in November 1978 near the natal territory from which it fledged in October 1976. The other five (juvenile-1, warbler-507, ♂-K, ♂-L and ♂-M) were males that I saw proclaiming territory. Four were of known age, having been banded as nestlings, while ♂-K was presumed to be juvenile when netted.

Juvenile-1 fledged on 5.i.1977 and was seen (by M. Powlesland) at the first location (Fig. 7.1) on 11.v.1977. Twice in November 1977 I saw this bird at the second location. It sang repeatedly, identifying itself as a male in possession of territory, but I did not determine whether it had a mate and bred. The territory was about 2.3 km from the nest (outside the main study-area) in which the bird was raised. Similarly, warbler-507 fledged from territory HU (Fig. 3.1c) on 19.x.1977,

and on 31.x.1978 I saw it singing on a territory (just outside the main study-area; not shown on any figure) nearly 800 m away.

Juvenile-14 = ♂-K (see section 3.3) was netted on 24.vii.1977, and seen repeatedly on a territory 400 m away, from 11.viii.1977 to 22.x.1977. Although this warbler sang regularly and fought with neighbouring males, it was probably non-breeding, since I never saw a mate. It apparently lost its territory for the second half of the breeding-season in 1977/78, and I next saw it in winter 1978. In 1978/79 ♂-K held a territory (Fig. 3.1d) throughout the summer and nested at least twice with an unbanded mate.

Juvenile-8 = ♂-M fledged on 11.x.1976 and had moved 500 m (Fig. 7.1) when I saw it on 12.v.1977, six months after independence. I next saw this bird in 1978, when it held a territory (Fig. 3.1d) from 27.viii.1978 until 25.x.1978 (at least), but I never saw a mate. The territory was 600 m from the nest from which ♂-M fledged.

Juvenile-17 = ♂-L fledged on 13.xi.1977 and had dispersed 460 m (Fig. 7.1) when I saw it on 8.ii.1978, less than two months after independence. In late August and early September 1978 ♂-L was on a territory (Fig. 3.1d) with an unbanded mate. I saw the female building, and the nest was 670 m from that in which ♂-L was raised. I did not determine whether eggs were laid, nor did I see ♂-L again - when I returned to the field in late October 1978 the territory was occupied by an unbanded pair.

Thus some male warblers (juvenile-1, warbler-507, ♂-K and ♂-L) held territory in the summer after that in which they were raised (their second summer). Observations of ♂-L further suggest that he was in reproductive condition nine months after fledging. However, both ♂-L and ♂-K failed to retain territory throughout their second summer, and ♂-K apparently did not attract a mate. On the other hand, ♂-K bred successfully two summers after fledging, and ♂-M may not have gained territory until his third summer. The evidence is meagre, but combined with the extreme rarity of recruitment, suggests that maturity may be deferred in grey warblers, perhaps by socio-environmental conditions, if not physiologically.

Nearly all terrestrial birds begin reproduction in the first breeding-season after that in which they were raised, but a few passerines, especially tropical species, breed in their second year, after deferred maturity (Lack 1968, Ricklefs 1973). Cody (1971) cited cases where age at first breeding was modified by environmental conditions.

8. GENERAL ASPECTS

8.1 BREEDING-SEASON, BREEDING-CYCLE AND FECUNDITY

In spring, the season for planting, grey warblers sing intensively. To a person who has cultivated no food one may quote the Maori proverb:

I hea koe i te tangihanga o te riroriro?
(Where were you when the grey warbler sang?)

(Colenso 1879)

Breeding-season

Fig. 8.1 shows seasonal details of major events in the breeding of the grey warbler and shining cuckoo (for discussion of the latter see section 12.1). The intensity of the warbler's song for the breeding half of the year (Fig. 8.1a) is from Cunningham (1955b). The horizontal axis (marked in quarter-months) differs from that of the other histograms (marked in weeks beginning 7-13 July). Cunningham quantified the seasonal intensity of the warbler's song at Masterton, by scoring the daily regularity of singing on a 3-point scale. He converted the daily records into weekly summaries (again on an arbitrary 3-point scale), and here 10 years' data are pooled to give a percentage intensity for each week. Fig. 8.1b gives the weekly frequency with which I saw warblers building at Kowhai Bush in 1976 and 1977 (see section 4.2). The weekly frequencies of laying, hatching and fledging of the warbler (Fig. 8.1d-f) are also for 1976/77 and 1977/78 combined at Kowhai Bush (see sections 5.2 and 6.2).

At Kowhai Bush grey warblers (males only) sang with variable intensity throughout the year. Cunningham's data (1955b) show that song is occasional in May, and that it increases through winter to reach maximum intensity in the last half of September. There is a second but smaller peak of song in the last half of November, and it is now clear that the two most intense periods of song coincide with the two main bouts of laying. After November song declines to a second minimum in January when breeding stops. Cunningham noted a slight increase in song during March which I cannot relate to an aspect of breeding. At Kowhai Bush grey warblers sang from both prominent and insignificant perches (presumably in proclamation and defence of territory), and near the nest at all stages of the reproductive cycle. They also sang while attending fledglings and at or near the nest in response to disturbance from other birds (especially bellbirds and robins), or man.

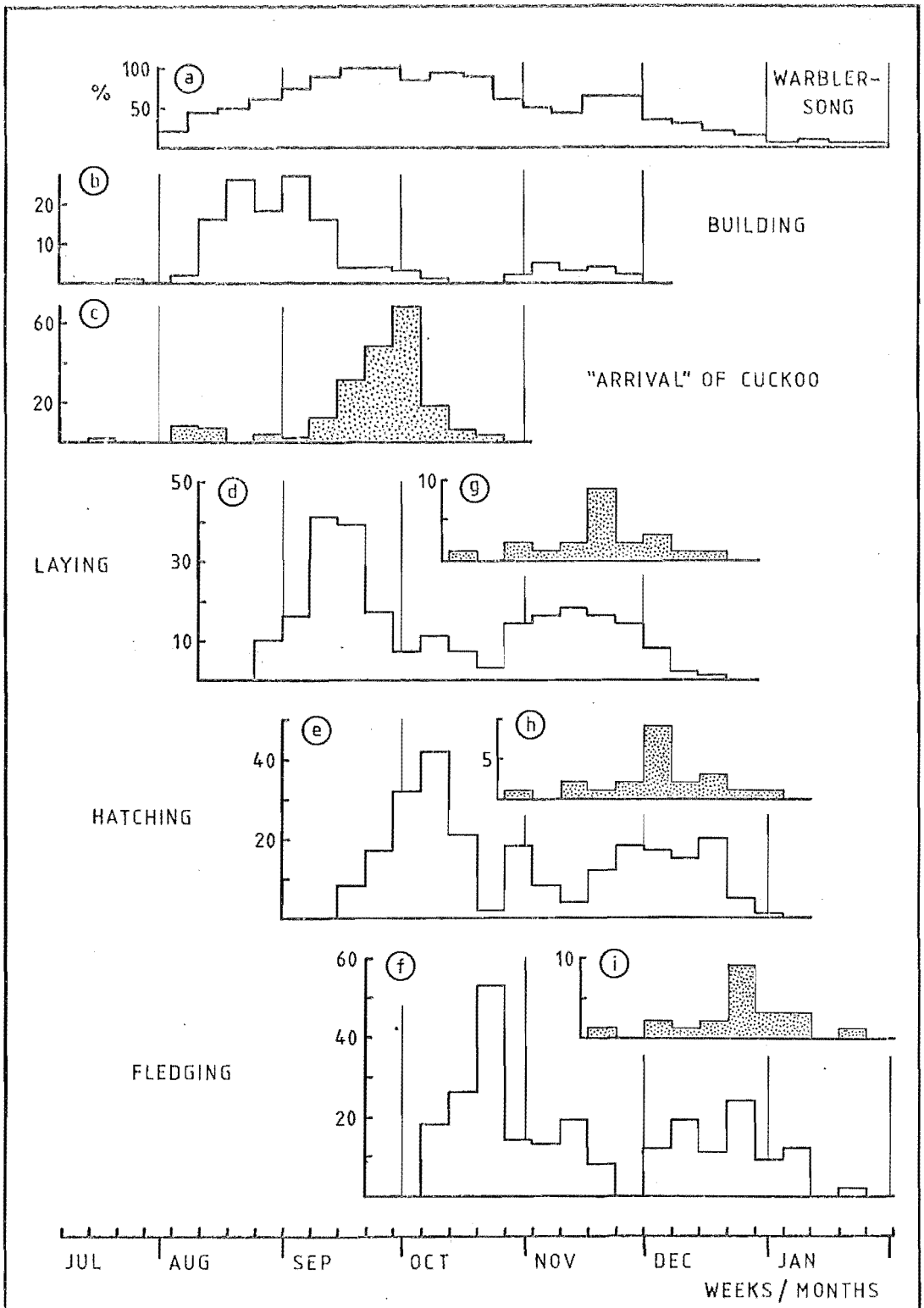

Figure 8.1 - Events in the breeding of host and parasite. (a) Intensity of warbler-song; (b) weekly frequency of building at Kowhai Bush (n = 134); (c) first reports of cuckoo-song in New Zealand (n = 212); weekly frequencies of laying/hatching/fledging of warblers (d-f, n = 240) and cuckoos (g-i, n = 22) at Kowhai Bush.

Bimodality in the warbler's breeding is clearly shown in the histograms of building, laying, hatching and fledging. Unfortunately I was uncertain whether both efforts in breeding were equal or whether some pairs stopped after rearing one successful early brood. Practical constraints in the field often prevented me from finding all the nests of certain pairs. However, the 16 pairs which I followed closest probably attempted to breed more than twice each (on average) per season.

The paucity of late building that I recorded was in disproportion to the number of nests actually found; an indication of the greater speed with which late nests were built (section 4.1).

The Nest Record Scheme provided 142 records of warbler-nests with sufficient details to indicate whether they were early (eggs before 23 October) or late (eggs after 23 October; or parasitised). The ratio of early : late nests (81 : 61) encourages the possibility that both are equally common, but that late ones are less often found.

The extremes of the breeding-season at Kowhai Bush (data for 1976/77 and 1977/78 combined) were from the last quarter of July, when I first saw building; to the third quarter of January, when the last nestling fledged. This season covered 27 weeks or six months. Data from the Nest Record Scheme (55 cards) gave similar extremes; the earliest recorded building was in early August and the last fledging in early January, apart from some exceptional cases (see sections 4.2, 5.2, 6.2). The breeding-seasons of other small native New Zealand passerines seem to be equally long (Appendix 1).

In temperate Australia, Acanthiza chrysorrhoa, Malurus cyaneus and Rhipidura leucophrys breed for at least as long as grey warblers and in the same months (from Ford 1963, Rowley 1965 and Marchant 1974). Meagre information on Gerygone in Australia indicates an August/September to January/February breeding-season (MacDonald 1973).

Exceptional warbler-eggs in mid-June (Nest Record Scheme; section 5.2) were laid before the shortest day (c. 20 June), which is surprising, although robins at Kowhai Bush occasionally lay before 20 June (Flack, in

preparation). Day-length at the laying of the first egg in my sample for Kowhai Bush was 10 hours 54 minutes, compared with 9 hours 10 minutes on 20 June. Passerines in the Southern Hemisphere apparently lay more commonly when days are 10-11 hours long than do species in the Northern Hemisphere (Baker 1938).

When grey warblers cease laying in mid-December the New Zealand summer has just begun, and when the last nestlings fledge in mid-January there are many weeks of warm weather ahead. Many British song-birds also stop breeding in summer long before their food is scarce (Lack 1950). Lack suggested three reasons for this:

a. If late juveniles are to survive they must fledge and become independent before food is short.
b. Adults need adequate food during their annual post-nuptial moult.
c. Adults of some species must accumulate fat before migration.

The first two points are relevant to the grey warbler and there is another factor, perhaps peculiar to New Zealand's situation, namely the drought in late summer. New Zealand's climate is liable to yearly fluctuations, there is an element of unreliability, and serious droughts in summer are common in many areas (Hurnard 1978). In January at Kowhai Bush the annual drought was often such that certain kinds of shrubs with large leaves wilted alarmingly for days, often weeks. At this time kanuka, the physiognomic dominant and the species from which warblers at Kowhai Bush obtain most food (Gill, in preparation), undergoes its greatest loss of leaves. The availability of food is probably such that mid- and late summer is a time for moulting rather than for breeding.

Adult warblers probably moulted only once annually, after breeding, as is typical of sedentary birds (Welty 1975: 38). Both retrices and body-plumage were apparently moulted in January, and certainly by March most birds had complete, unworn tails.

Breeding-cycle

The length of the breeding-cycle is expressed by adding the days required to lay a clutch to the incubation and nestling periods. For the warbler's modal clutch of four the breeding-cycle is 43.7 days (7 + 19.5 + 17.2 days). Among New Zealand passerines this is almost the same as for *Petroica australis*, slightly longer than for *Bowdleria punctata* and much longer than for *Rhipidura fuliginosa* (Appendix 1). In temperate Australia the breeding-cycles of *Acanthiza chrysorrhoa*,

Rhipidura leucophrys and Malurus cyaneus are about 42, 31 and 30 days respectively (from Ford 1963, Rowley 1965, Marchant 1974).

To determine the average time between laying of a first egg by a pair of warblers, and fledging of their second successful brood, we must double the breeding-cycle (43 days) and add 23 days for the average delay between fledging of the first brood and initiation of the second clutch (section 5.9; n = 7). This value, for individuals, is 109 days, but the population of warblers laid asynchronously during about 40 days (section 5.2). Thus the period during which eggs and nestlings would occur if pairs raised no more than two successful broods is about 150 days. The earliest date of laying that I recorded at Kowhai Bush was 25 August, and the latest date of fledging was about 22 January, 150 days later. Therefore, within the observed limits of the breeding-season, there is no time for a pair of warblers to raise more than two successful broods.

Other New Zealand passerines may raise three successful broods per season (Appendix 1), either because their breeding-season is long and time taken to build short (*P. australis*), or because all events in breeding are performed relatively quickly (*Z. lateralis*). In Australia Acanthiza chrysorrhoa raises 1-4 broods per year and Malurus cyaneus 2-3. However, both species have helpers at the nest.

Fecundity

The annual fecundity of multi-brooded birds (number of clutches laid and broods raised per year) is poorly known (Ricklefs 1973). I was unable to follow closely all marked warblers in my study-area throughout their breeding-season, but 16 pairs probably built nests (and laid) a total of 37 times. Thus the average number of nesting-attempts was 2.3/pair/year.

The fecundity of grey warblers calculated indirectly (Ricklefs 1973: 401) was 3.1 nesting-attempts/pair/season. This is probably an over-estimate since it assumes that every pair re-nested throughout a season, the extent of which was set by dates of first and last breeding for the whole population. The direct estimate of fecundity, however, may be conservative because I assumed that many pairs did not re-nest close to the season's end, so I favour the mean (2.7). In monogamous species where both sexes feed the young the annual productivity of fledglings per individual (P)

= (nesting-attempts/pair x no. eggs/clutch x breeding-success)/2

= (2.7 x 3.93 x 0.38*)/2 for grey warblers

= 2.02 fledglings/individual/year.

In a stable population, the proportion of fledglings which must survive to breed and so balance the mortality of adults, is given by adult mortality (section 3.6) over P' (Ricklefs 1973). For warblers this figure is 0.19/2.02 = 0.09, which is less than values cited by Ricklefs for north-temperate song-birds - 0.16 in *Melospiza melodia* and *Turdus merula*, 0.13 in *Parus major*. Both dividend and divisor are higher in the latter than for grey warblers (eg. 0.5/3.2 in *Melospiza*).

The calculated annual recruitment of juvenile warblers (9%) is close to the observed recruitment in the main study-area (5% per annum; section 7.4).

* section 8.2

8.2 MORTALITY AND REPRODUCTIVE SUCCESS

Grey warblers failed to lay in two of 90 fully-constructed nests. One was an early nest, the other was late, and at least in the former the male apparently lost his mate at the time eggs were due. I found two further nests abandoned at an early stage of construction, perhaps through indecision in siting them. Of nests that received eggs, Table 8.1 gives the proportions that later held nestlings or yielded fledglings. For example, of 46 sufficiently documented early nests, 83% contained nestlings on some occasion, so 17% did not proceed beyond holding eggs. The data reflect both the "survival" of nests and the often independent survival of the eggs and young within.

Table 8.1 - Success of nests that received eggs, in terms of the proportion that later held nestlings or yielded fledglings (data for three years combined). A. warblers and cuckoos treated as one; B. cuckoos treated as failure.

		held eggs	held nestlings	%	held eggs	yielded fledglings	%
	early	46	38	83	42	26	62
A.	late	41	33	81	40	18	45
	all	87	71	82	82	44	54
B.	late	35	27	77	40	8	20
	all	81	65	80	82	34	42

At Kowhai Bush, 42% of nests yielded at least one fledgling warbler. Similarly, of 44 nests reported to the Nest Record Scheme with the necessary details, 20 (46%) were successful (at least one warbler fledged or seemed likely to). Of 521 nests of *Petroica australis* at Kowhai Bush, 35% yielded at least one fledgling (Flack and Lloyd 1978). In Dunedin 80% of silvereye-nests were successful (Kikkawa 1966).

Predation is the most important cause of mortality in small landbirds (Ricklefs 1973). No avian predators of warbler-nests are known, though the shining cuckoo may be one. *Cuculus canorus* avidly preys on

eggs and even nestlings (Wyllie 1975), and Fulton (1910) was convinced of shining cuckoos being predatory. In Northland, Michie (1948) apparently saw shining cuckoos consuming the contents of warbler- and chaffinch-eggs. In Australia, Fien (1970) saw the removal of a nestling *Malurus* by *Chrysococcyx basalis*. Moon (1960) suggested that magpies (*Gymnorhina*) may prey on the contents of warbler-nests. Of mammals there are six obligately or facultatively predacious species at Kowhai Bush (Moors 1975 and pers. comm.): three mustelids (weasel, *Mustela nivalis*; stoat, *M. erminea*; and ferret, *M. putorius* forma *furo*), two rodents (ship rat, *Rattus rattus* and mouse, *Mus musculus*) and the feral cat (*Felis catus*). Of these, ferrets do not climb, so can be discounted as nest-predators.

Previous research at Kowhai Bush showed that most predation of robin-nests is due to mustelids (Moors 1975), which hunt at any height actively seeking out nestlings. Rodents eat both eggs and nestlings, apparently after stumbling across low nests during nocturnal foraging (Flack and Lloyd 1978). In robbing the cupular nests of robins, rodents disarrange them and leave a scattering of partly-eaten eggs and nestlings. Stoats and weasels, however, leave nests structurally undisturbed and with little or no remains of the contents (Moors 1975).

Of 82 warbler-nests at Kowhai Bush, 38 received eggs but did not yield fledglings (warbler or cuckoo; from Table 8.1). Of these nests, evidence of predation attended the failure of 12 (32%). Ten were structurally damaged, implicating large stoats, ship rats or cats. (In view of the small entrance to warbler-nests, probably only weasels, small stoats and mice could prey upon the contents without damaging the nest.) Four nests were severely damaged (even completely torn to shreds) and there were scattered egg-shells or mutilated remains of nestlings on the ground directly beneath. These were probably destroyed by ship rats. Six nests were torn at one side and their contents were gone. Mustelids (particularly stoats) probably caused the loss of these. At two other nests feathered young were preyed upon without damage to the nest. Some of these nestlings were killed but not eaten; others were unharmed on the ground, but when returned to the nest were killed or disappeared days later. Since mustelids are highly efficient predators, these nests were probably disturbed by rats.

The mean height of 10 preyed-upon nests was 2.7 m, compared with 3.2 m for all nests (section 4.4). The mean ratio of nest-height: canopy-height was 0.32 (n = 10), compared with 0.38 for all nests.

However, neither difference was significant (t-test). Of 10 preyed-upon nests 40% were truly pensile, as were 46% of all nests (Appendix 2), so it appears that predation was a random event with respect to these characteristics. The average height of robin-nests preyed upon at Kowhai Bush was similar to that of successful nests (Moors *et al.*, in preparation).

At Kowhai Bush mammalian predators robbed 44-66% of robin-nests (Moors *et al.*, in preparation), whereas only 12 (15%) of 82 warbler-nests receiving eggs were affected. This probably reflects the safer nest of warblers, but I blamed predation only when the nest was damaged or I found wounded nestlings. At other nests eggs and young disappeared or I found damaged eggs, possibly as a result of additional predation.

The known or inferred causes of mortality of 79 eggs and 72 nestlings which did not survive are given in Tables 8.2 and 8.3 respectively.

Table 8.2 - Fates of eggs which failed to hatch (1976/77 and 1977/78).

	1976/77		1977/78		early		late		overall	
cause of mortality	no.	%	no.	%	no.	%	no.	%	no.	%
infertility	4	12.5	4	8.5	6	16.7	2	4.6	8	10.1
death of embryo	6	18.8	7	14.9	6	16.7	7	16.3	13	16.5
cuckoo-parasitism: removal	5	15.6	6	12.8	0	-	11	25.6	11	13.9
cuckoo-parasitism: eviction	3	9.4	3	6.4	0	-	6	14.0	6	7.6
? : disappearance	9	28.1	16	34.0	11	30.6	14	32.6	25	31.7
? : eviction	4	12.5	10	21.3	12	33.3	2	4.6	14	17.7
? : broken in nest	1	3.1	1	2.1	1	2.7	1	2.3	2	2.5
n	32		47		36		43		79	

One unhatched egg in 10 was infertile, containing no trace of an embryo. Infertility was more common in early clutches, suggesting poor behavioural or physiological synchronisation during some initial matings. Death of embryos, due to unknown causes, was a constant and significant source of failure.

Parasitism of clutches by the shining cuckoo caused loss of eggs in two ways: the cuckoo's egg was apparently substituted for a warbler's, the latter being removed (section 10.1), and nestling cuckoos evicted warbler eggs (section 11.2). Taken together these factors were an important cause of mortality overall (21.5%), and the major factor (39.6%) for late clutches.

About a third of eggs failing to hatch at any time disappeared without trace - in many cases probably due to predation by introduced mammals. Eggs vanished all at once or sporadically, and sometimes only part of a clutch disappeared. Some eggs missing from late clutches may have been removed by cuckoos, but this seems unlikely since as many disappeared from early clutches, at which time cuckoos are still arriving in New Zealand (Fig. 8.1).

The presence of eggs on the ground beneath nests, other than those evicted by cuckoos, was particularly common for early clutches in 1977. At this time strong winds seemed responsible for the loss of nine eggs; at other times predation was a likely cause. Two eggs broken in the nest may also have been preyed upon. Conceivably, the adult warblers may have caused the disappearance, eviction and breakage of some of their eggs.

The greatest single cause of mortality of nestlings (Table 8.3) was predation, indicated by destruction of the nest or mutilation of nestlings. Nearly equal in importance to predation were both the disappearance and death of young for unknown reasons, among which unrecognised predation may have been significant. More nestlings disappeared in 1976/77 than in the following year, and more died in the nest in early broods than in late ones. Eviction, other than by cuckoos, refers to some nestlings in 1977/78 found unharmed on the ground beneath their nests, perhaps after disturbance by a predator.

Eviction of nestling warblers by young cuckoos affected only late broods and was apparently more important in 1977/78 than in the previous year. Parasitism by cuckoos was a major cause of mortality for late broods but a relatively minor one for nestlings overall. The last nestling to hatch in two early broods of four in 1976 failed to gain weight and died, while the respective siblings remained healthy. These were apparently "runts" which starved.

Early and late nests with eggs at Kowhai Bush were equally likely to contain nestlings (warbler or cuckoo; Table 8.1), but late nests with eggs were much less likely to yield fledglings (warbler or cuckoo) than

Table 8.3 - Fates of nestlings which failed to fledge (1976/77 and 1977/78).

cause of mortality	1976/77		1977/78		early		late		overall	
	no.	%	no.	%	no.	%	no.	%	no.	%
? : death in nest	10	24.4	7	22.6	14	42.4	3	7.7	17	23.6
cuckoo-parasitism: eviction	3	7.3	9	29.0	0	-	12	30.8	12	16.7
? : disappearance	14	34.2	3	9.7	9	27.3	8	20.5	17	23.6
? : eviction	0	-	4	12.9	0	-	4	10.2	4	5.5
predation	12	29.3	8	25.8	8	24.2	12	30.8	20	27.8
competition? : "runts"	2	4.8	0	-	2	6.1	0	-	2	2.8
n	41		31		33		39		72	

early ones. Factors other than brood-parasitism must have been responsible for the increased mortality of nestlings in late as against early nests. No factors (apart from parasitism) bore more strongly on late warbler-eggs than on early ones (Table 8.2), but eviction of warbler-nestlings (cause unidentified) and predation, increased for late broods (Table 8.3). Late in the season rodents multiply in number at Kowhai Bush and mustelids raise their litters (P. Moors, pers. comm.).

Predation of robin-nests at Kowhai Bush also increases as the breeding-season progresses (Moors 1975).

Nestlings which died in the nest without obvious cause were probably not preyed upon, since mostly early broods were affected (Table 8.3). The cause of this mortality may have been an absolute shortage of food early in the season (though some of the dead nestlings I dissected had full stomachs), a relative shortage of high-quality food, or a combination of these and other factors such as weather and disease. Nestlings 0-9 days old in early broods were lighter on average than those in late broods (section 6.5), providing circumstantial corroboration.

Table 8.4 and Fig. 8.2 give the reproductive success of warblers in early and late nests for three years. Parasitised nests were counted as failures

Table 8.4 - Reproductive success of warblers and cuckoos (C).

		nests	eggs laid	young hatched	young fledged	success (%) hatching-	breeding-	nestling-
1976/77	early	18	65	60	38	92.3	58.5	63.3
	late	13	44	25	9	56.8	20.5	36.0
	total	31	109	85	47	78.0	43.1	55.3
	C	8	8	4	3	50.0	37.5	75.0
1977/78	early	18	70	45	36	64.3	51.4	80.0
	late	15	53	32	10	60.4	18.9	31.3
	total	33	123	77	46	62.6	37.4	59.7
	C	8	8	8	5	100.0	62.5	62.5
1978/79	early	4	15	11	2	73.3	13.3	18.2
	late	5	18	12	5	66.7	27.8	41.7
	total	9	33	23	7	69.7	21.2	30.4
	C	7	7	4	4	57.1	57.1	100.0
all years	early	40	150	116	76	77.3	50.7	65.5
	late	33	115	69	24	60.0	20.9	34.8
	total	73	265	185	100	69.8	37.7	54.1
	C	23	23	16	12	69.6	52.2	75.0

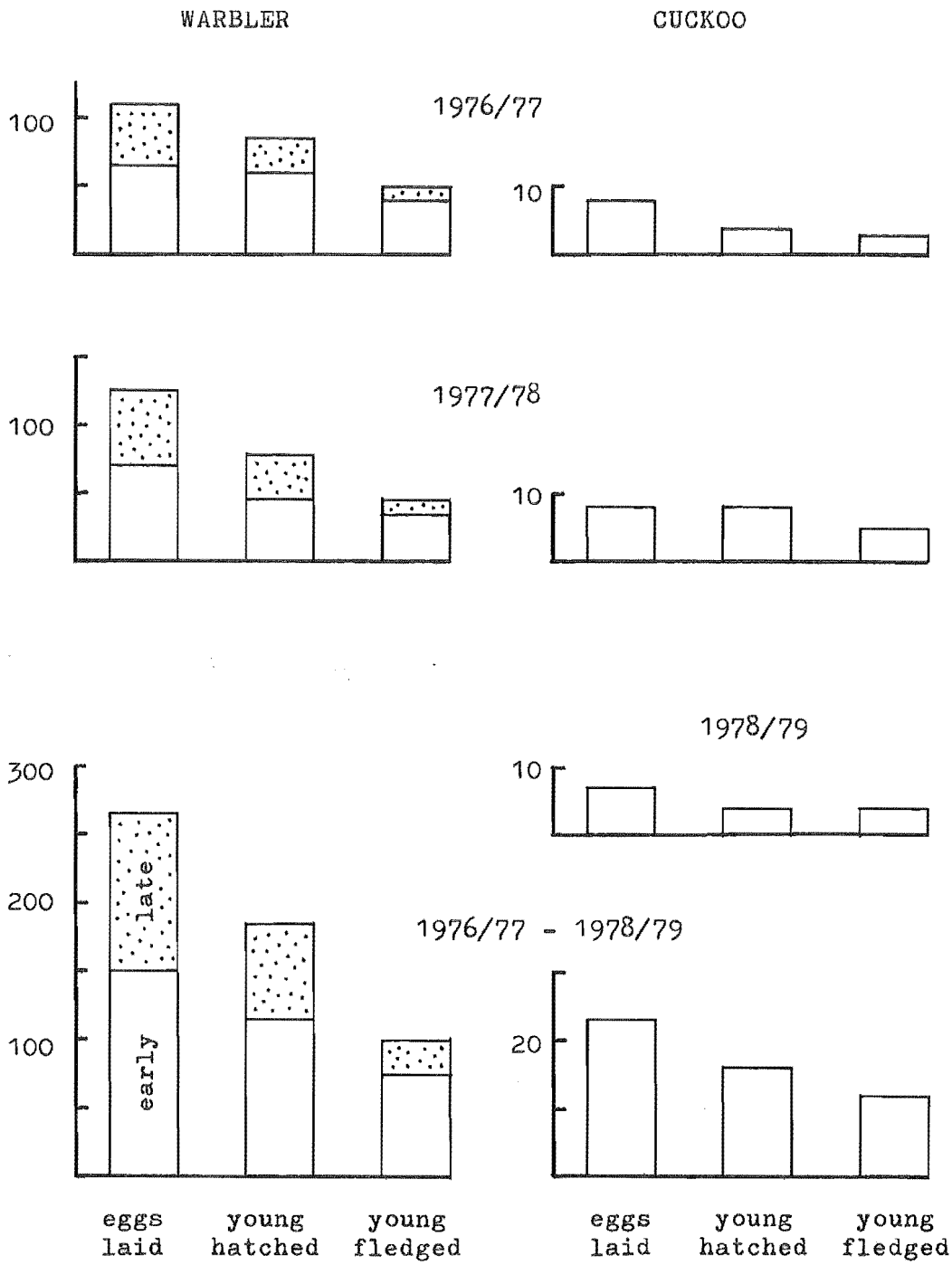

Figure 8.2 - Reproductive success of warblers and cuckoos (see Table 8.4).

from the warbler's point of view, and success for cuckoos is discussed in section 12.3. Hatching-success is the proportion of eggs which hatched, breeding-success the proportion of eggs which hatched to eventually yield fledglings, and nestling-success the proportion of nestlings which fledged.

In every year a smaller proportion of eggs hatched in late nests than in early ones, and, except in 1978/79 when samples were small, breeding- and nestling-success were also lower for late nests. This is further expression of the small probability of late nests yielding fledgling warblers (Table 8.1), and is caused by brood-parasitism, and an increase in predation by mammals, in the second half of the breeding-season.

Except for early nests in 1977/78, hatching-success was greater than nestling-success, indicating that nestlings had much less chance of survival than eggs. This is especially so considering that the nestling period (17.2 days) was shorter than the incubation period (19.5 days). Nestlings cheep, cause both parents to visit the nest frequently, and are probably thus more attractive of predators than eggs. Causes of mortality likely to involve predation accounted for 81% of unfledged nestlings but only 52% of unhatched eggs (from Tables 8.2 and 8.3).

The success of late nests (all three expressions; Table 8.4) was similar in 1976/77 and 1977/78. However, while the success of early eggs was high in 1976/77, and that of early nestlings low, the converse was true in 1977/78, though the net result (early breeding-success) was similar in both years. This corroborates findings in section 6.3.

In total, of 265 warbler-eggs laid in 73 nests at Kowhai Bush, 70% hatched and 38% eventually produced a fledgling. Of 185 nestlings, 54% fledged. Thus, despite the enclosed and often pensile nest, grey warblers have low reproductive success. Brood-parasitism is a relatively minor cause of mortality (section 12.5), and although clear evidence was often lacking, probably the greatest single factor detrimental to the warbler's reproductive effort was disturbance by introduced rodents and mustelids.

Table 8.5 gives reproductive success for a range of passerines. Robins at Kowhai Bush were reproductively less successful than warblers, probably because the nest is cupular and located in sites more accessible to predators. Silvereyes in Auckland bred more successfully than warblers, but the data were from only 11 nests. Silvereyes often semi-suspend their nests relatively inaccessibly at the tips of branches. Not surprisingly, warblers at Kowhai Bush had lower success than black

Table 8.5 - Reproductive success of Australasian passerines. Type of nest: C = cupular, E = enclosed, H = in a hole.

		nest	success (%) hatching-	breeding-	nestling-	no. eggs
Gerygone igata[1]	Kowhai Bush	E	70	38	54	265
Petroica australis[2]	"	C	63	26	42	407
Zosterops lateralis[3]	Auckland	C	86	70	-	30
P. macrocephala[4]	Snares Is.	C	87	56	64	54
Bowdleria punctata[4]	"	C	54	32	60	79
Malurus cyaneus[5]	Australia	E	66	54	82	240
Acanthiza chrysorrhoa[6]	"	E	65	52	80	324
Rhipidura leucophrys[7]	"	C	81	57	71	520

Sources: 1 present study; 2 R. Powlesland, pers. comm.; 3 Fleming (1943); 4 Best (1975); 5 Rowley (1965); 6 Ford (1963); 7 Marchant (1974).

tits on the Snares Islands where there are no introduced mammals. Snares fernbirds had low hatching- and breeding-success because some nests were built in flimsy ground-vegetation and were disturbed by shearwaters which crash-landed on the island at night (Best 1975).

The hatching-success of warblers was slightly higher than for *Malurus* and *Acanthiza* (Table 8.5), but lower than for the Australian *Rhipidura*. Breeding- and nestling-success were much lower in warblers than in Australian counterparts.

8.3 DISCUSSION

Breeding-strategy of the Grey Warbler

Grey warblers breed slowly. The long laying-season starts early and asynchronously. Warblers take a long time to build an early nest and there is a delay before laying. The long breeding-cycle (laying-interval, incubation period, nestling period) precedes a delay before re-laying and a long period of juvenile dependency. Coupled with the double-broodedness of warblers, the non-participation of the male in building and incubation, and his not feeding the female, these factors are circumstantial evidence that the breeding-strategy may be adapted to a relative shortage of food during the breeding-season. If food is short, and a mild climate and lack of predators permits (as in New Zealand), it may be advantageous for birds to raise several small broods slowly during a long breeding-season, rather than to rear fewer larger broods quickly. Warblers seem to have evolved the former strategy.

The lowlands of New Zealand are equable and moderate (see Hurnard 1978), and there is no marked seasonality. These are tropical characteristics, or at least features far removed from those of temperate continental climates. Plants of the lowland native forest in New Zealand may grow continuously or for protracted periods (Wardle 1978). The seasonal abundance of native invertebrates is not known, but the quantity of food, especially non-flying insects, available to insectivorous birds in lowland forest may vary little throughout the year and may not decline severely in winter. Grey warblers, which glean arthropods from foliage, may respond to their food-supply more in the way suggested for tropical land-birds, than in the way of north-temperate song-birds.

Ashmole (in Lack 1968) pointed out that in the Northern Temperate Zone numbers of sedentary insectivorous song-birds are reduced by a severe shortage of food in late winter. (For example, Gibb (1960) found that populations of titmice in English pine-plantations declined during winter to an extent closely correlated with the size of the stock of food at the time.) With the flush of invertebrates coinciding with the breeding-season in spring, surviving birds and returning migrants raise large families. Food-supply in the tropics, however, is virtually constant and populations remain close to the limit set by food. Extra food is hard to obtain at any time, so that during breeding only small families are raised.

Given the long breeding-season and high longevity of grey warblers, clutches may be smaller than a hypothetical congener with a shorter breeding-season at the same latitude would produce. Unfortunately, the clutch-size and breeding-season at a specific locality are not reported in detail for any other *Gerygone*. Furthermore, general accounts (e.g. MacDonald 1973) suggest that breeding-seasons of temperate Australian *Gerygone* are the same as for grey warblers.

The hypothesis that a long breeding-season, high longevity and small clutch-size have evolved together in New Zealand land-birds received support from Niethammer (1970). He showed that 10 species of introduced passerines had, or appeared to have, significantly smaller average clutches in New Zealand than in Britain, their country of origin. Also, a single banding-study in New Zealand produced longevity records for introduced song-birds approaching, and even exceeding, those recorded for the same species during the entire history of banding in Europe. On average New Zealand is 12° of latitude closer to the equator than Britain. However, Niethammer rejected a latitudinal explanation of the small clutches in New Zealand because there was no difference in average clutch-size of *Turdus merula* or *T. philomelos* between northern and southern parts of the country. Instead he attributed the small clutches of British song-birds in New Zealand to high densities and a consequent shortage of food.

The large egg of grey warblers (which may be the immediate cause of the unusual laying-interval) produces a large hatchling, perhaps with a lessened demand for the small and nutritious items of food which would otherwise be required (see Lack 1968). Thus the egg may be adapted to suit unpredictable conditions. Given the small size of warblers and a possibly unpredictable food-supply, the heaviness of nestlings relative to adult weight (apparently caused by a temporary accumulation of water) may be an adaptation to increase mass and so conserve heat.

The low annual mortality of adult warblers and the long life-expectancy is probably made possible by the low recruitment of juveniles and an attendant lessening of intraspecific competition. The low fecundity and reproductive success is probably due partly to the recent introduction to New Zealand of mammalian predators. There were (and are) no terrestrial snakes in New Zealand, nor were there predatory mammals until introductions by man of rodents, mustelids and cats (Gibb and Flux 1973). Falcons (*Falco novaeseelandiae*) prey on adult warblers (Fox 1977), and Hay (1978) saw a kingfisher (*Halcyon sancta*) with a warbler in its bill held by the tail, but there are no confirmed avian predators of warbler nests.

One assumes that a lack of predators was critical in permitting a long, extended breeding-cycle in warblers. However, the assumption is weakened by the slow breeding of some Australian passerines (e.g. *Acanthiza chrysorrhoa*) which evolved in the presence of many predators. Retention of the enclosed nest by warblers in the absence of predators may have been for the nest's possible adaptive value in insulation, or because there was no pressure to modify the nest and little cost in retaining it.

Predation of nests is greatest in the tropics, and Skutch (1949, cited by Cody 1966 and Owen 1977) postulated that tropical passerines raise small families slowly to reduce the frequency with which parents visit the nest, thus minimising the chance of attracting predators. That grey warblers raise small families slowly in a region (formerly) free of predators, suggests that Skutch's hypothesis is not general (D. Dawson, pers. comm.).

Comparisons between Grey Warblers and Other Passerines

A. New Zealand

Though the rifleman (*Acanthisitta chloris*) is familially endemic to New Zealand and the grey warbler not even generically so, the two species share a remarkably similar breeding-strategy. They have heavy eggs and nestlings relative to body-weight, the same laying-interval, and long breeding-cycles (Appendix 1). Riflemen differ from warblers in being tyrannine rather than oscinine birds,and by nesting in holes, but both are entirely insectivorous and are the smallest New Zealand birds. The similar breeding-strategies may derive from common energetic problems related to small size and a possibly unpredictable food-supply.

Studies of the other native passerines (Appendix 1) indicate that whereas the unusual laying-interval and growth of warblers may not be general, the long breeding-season, small clutch-size and long incubation and nestling periods probably are. Much more work is needed.

B. Temperate Australia

Comparisons between grey warblers and counterparts in temperate Australia are limited by a lack of detailed information on the latter. No accounts of breeding in *Gerygone* have been published, but Ford (1963) studied the yellow-tailed thornbill (*Acanthiza chrysorrhoa*) in south-western Australia, and Rowley (1965) the superb blue wren (*Malurus cyaneus*) near Canberra; both species are close relatives of *Gerygone*. They have enclosed nests, but differ from grey warblers in

social structure: progeny from a previous brood, and non-breeding adults, often assist a breeding pair to feed nestlings. The thornbill is very close to the grey warbler in details of breeding, while the wren, less closely allied to *Gerygone*, differs from the warbler on several points such as laying-interval and length of breeding-cycle. Data on other related temperate Australian song-birds come from analysis of nest-records (Courtney and Marchant 1971, Marchant 1974) and are incomplete.

Generally, the adaptations for breeding that characterise temperate Australian passerines are (1) small clutches (usually 2 or 3 eggs), (2) 48-hour laying-intervals, (3) delayed laying after nest-building, (4) high longevity, (5) helpers at the nest, and (6) nomadism outside the breeding-season (Thomas 1974). Points 1 to 4, but not 5 and 6, are shared by grey warblers. However, clutch-size is apparently slightly higher in warblers than in Australian relatives, and laying is often delayed for several weeks in Australia compared with up to eight days in warblers. Thomas suggested that the breeding strategies of temperate Australian land-birds may be responses to a food-supply that is "never abundant", which is similar to my own interpretation of the grey warbler's breeding.

C. The Northern Temperate Zone

Comparisons between grey warblers and song-birds of mid-Europe and much of North America are risky because of many uncontrolled variables such as the discrepancy in latitude, inherent differences in climate and the uncertain relatedness of birds in different geographic areas.

The following general points emerge. Annual adult mortality is higher for north-temperate species than for grey warblers. Unlike warblers, most small northern passerines usually build nests in only a few days (2-20 days for nine species cited by Welty 1975), and typically they delay before laying for only 1-4 days (Davis 1955). Many north-temperate passerines lay all their eggs, or at least first clutches, synchronously during a few weeks at most (Gibb 1950, Summers-Smith 1952, Dunnet 1955, Lack 1966). All song-birds studied in the Northern Hemisphere lay eggs of a clutch 24-hours apart. Eggs and nestlings as heavy relative to adult weight as those of the grey warbler are unknown among arboreal insectivorous north-temperate passerines.

Average clutch-sizes in mid-European song-birds (Lack 1948) with enclosed nests (6.8) and cupular nests (5.1) are larger than in grey warblers. So too are the average clutches of United States hole-nesters (5.4), but mean clutch-size is only 4.0 in U.S. cup-nesters (Nice 1957). The warbler's incubation period is longer on average by six days than mean values for north-temperate song-birds irrespective of nest-type (Lack 1948, Nice 1957). Only U.S. hole-nesters among north-temperate song-birds have on average a longer nestling period (18.8 days, Nice 1957) than the warbler.

The warbler's breeding-cycle (44 days) is longer than the average for north-temperate hole-nesting passerines (38 days), and for species with cupular nests in Europe and the United States (31 and 27 days on average respectively; Nice 1957). Warblers have a hatching-success about the same as for cup-nesting and hole-nesting north-temperate altricial birds, but the breeding-success is generally lower.

Many of these contrasts between grey warblers and north-temperate counterparts undoubtedly arise because the latter are responding to a food-supply influenced by shorter summers and more severe winters than experienced in New Zealand. Also, many north-temperate species must expend energy in migrating long distances before and after breeding, which is required of no New Zealand passerines.

PART 2 - BREEDING OF THE SHINING CUCKOO

9. PRELIMINARIES

9.1 INTRODUCTION

Birds which lay in the nests of other species, and use these hosts to incubate the eggs and rear the young, are termed brood-parasites.

Brood-parasitism has evolved independently seven times in birds, and is practised by about 80 species or 1% of the world's avifauna (Lack 1968: 82, Payne 1977). It is known in cowbirds (Icteridae), the cuckoo-weaver (Ploceidae: Ploceinae), widowbirds (Ploceidae: Viduinae), Old World cuckoos (Cuculidae: Cuculinae), three South American cuckoos (Cuculidae: Neomorphinae), honeyguides (Indicatoridae) and in a duck (Anatidae).

The family Cuculidae of the order Cuculiformes has seven sub-families (Meise and Schifter 1972), of which the Cuculinae is largest, comprising the 50 true parasitic cuckoos that are widely distributed in the Old World (Thomson 1964: 170). Cuckoos (Cuculinae) have zygodactylous toes and vary in length from 15 cm to over 60 cm. Many eat warningly-coloured, hairy and partly-toxic caterpillars, and most parasitise passerines smaller than themselves (Lack 1968: 82).

Two cuckoos breed in New Zealand and four other species (two *Cuculus*, a *Cacomantis* and a *Scythrops*) are rare stragglers (Kinsky 1970). The breeding cuckoos apparently parasitise New Zealand's five malurine warblers (Muscicapidae). The long-tailed cuckoo or koekoea (*Eudynamis taitensis*) is said to parasitise the whitehead (*Mohoua albicilla*) in the North Island, and the yellowhead (*M. ochrocephala*) and brown creeper (*Finschia novaeseelandiae*) in the South; while the shining cuckoo or pipiwharauroa (*Chrysococcyx lucidus lucidus*) parasitises the grey warbler (*Gerygone igata*) on the main islands and the endemic warbler (*G. albofrontata*) on the Chathams (Oliver 1955). The cuckoos are the only birds in the terrestrial avifauna which migrate beyond New Zealand. They breed in New Zealand during summer, and spend the New Zealand winter

on tropical islands of the western Pacific.

The shining cuckoo belongs to one of a group of 12 species distributed throughout SE Asia, Australasia and Africa south of the Sahara (Friedmann 1968). The group is characterised (with one exception) by iridescent plumage - hence the general name glossy cuckoos - and its members are the smallest birds of the sub-family, if not the order. Taxonomists with largely regional interests grouped the four African species as *Chrysococcyx*, placed the non-glossy *osculans* of Australia in a monotypic genus *Misocalius*, and referred the remaining seven Indo-Australian species to *Chalcites* (Friedmann 1968). The New Zealand Checklist (Kinsky 1970) follows this, but Berger (1955) compared the anatomy of several glossy cuckoos (including *lucidus*) and concluded that all are congeneric, and referrable to *Chrysococcyx* by the law of priority. This interpretation is widely accepted (eg. Friedmann 1968, Marchant 1972, Harrison 1973).

Four sub-species of *Chrysococcyx lucidus* have been described, of which the shining cuckoo is the nominate race, named by Gmelin (1788). The Australian race - *Ch. lucidus plagosus* (Latham, 1801) - is migratory like the shining cuckoo, but there are also two sedentary races. *Ch. lucidus layardi* (Mathews, 1912) occurs on New Caledonia and the New Hebrides, and *Ch. lucidus harterti* from Rennell and Bellona Islands (immediately SE of the Solomon-group) was described from five specimens by Mayr (1932). The shining cuckoo is said to winter on the Solomon Islands, 3 000 km from New Zealand (Mayr 1932).

Mayr (1932) gave the weights of four shining cuckoos from the Solomon Islands (some immature; means of preservation not stated) as 23, 25, 28 and 34 g ($\bar{x}$ = 27.5 g). The average weight of 16 adult cuckoos (which had been frozen and thawed) from New Zealand was 23.1 g (s = 2.77, range = 18.0-27.5 g). Thus the parasite is about four times heavier than its host (6.4 g). I could not distinguish the sexes of 22 dead adults except by dissection. MacDonald (1973) stated that the sexes are alike in *Chrysococcyx lucidus*, but others (eg. Mayr 1932, Oliver 1955, Falla *et al.* 1970) have claimed, at least for some races, that they are sexually dimorphic.

9.2 HOSTS

Friedmann (1968) relied on published records and egg-collections in summarising the hosts involved in hundreds of cases of parasitism by *Chrysococcyx*, and was aware of the bias towards the unusual in his lists. Cuckoos occasionally parasitise hosts accidentally, and Jensen and Jensen (1969) distinguished "biological hosts" (which are known to have hatched cuckoos) from "egg-hosts" (in whose nests cuckoo-eggs, but not young, have been recorded). Marchant (1972) believed that many, if not all, records of unusual hosts listed by Friedmann may be discounted. He drastically reduced the lists of fosterers given by Friedmann for *Ch. basalis* and *lucidus plagosus*, as did Jensen and Jensen (1969) for *Ch. klaas* and *caprius*. *Ch. lucidus plagosus* allegedly parasitises 75 species, with a preference for *Acanthiza* and to a lesser extent *Gerygone* (Friedmann 1968), but Marchant (1972) suspected that it is "quite strongly host-specific to *A. chrysorrhoa*".

There is general agreement that the grey warbler is the shining cuckoo's primary host throughout mainland New Zealand, but nearly every author on the subject has listed up to nine other species which the cuckoo supposedly parasitises. For example, Oliver (1955) stated that eggs of the shining cuckoo have been reported in the nests of *Rhipidura fuliginosa*, *Petroica macrocephala*, *Zosterops lateralis*, *Passer domesticus* and *Fringilla coelebs*. The other alleged hosts are: *Mohoua albicilla*, *Petroica australis*, *Turdus merula* and *Anthornis melanura*.

Most of these records I have traced to their earliest source in the literature. Fantail was given as a host, without substantiation, by Dieffenbach (1843: 194). Buller (1888) mentioned *Rhipidura* as a host, but only in connection with *Chrysococcyx lucidus* in Australia. Potts (1884: 287) claimed to have a record of tomtit being parasitised, but he gave no details. Blackbird was listed by Fulton (1910) with reference to Dieffenbach (1843), but I can find no mention of it in the earlier publication. The record for silvereye is due to Potts (1885: 477-8) who advanced it with reservation. He collected a silvereye's clutch of four which included a "bluish-green" egg that he considered might have been a cuckoo's. (Silvereyes have pale blue eggs; Falla *et al.* 1970). In November 1978 I found a silvereye's nest at Kowhai Bush containing four eggs identical in colour but not in shape. One egg was elliptical, rather than oval, and I wondered if it belonged to some cuckoo that had perfected mimicry of the silvereye's eggs. However, at a later visit the nest contained four nestling silvereyes.

The inclusion of bellbird as a host may have its origin with Buller (1888), who gave a second-hand report of a young cuckoo (presumably a fledgling) being fed by a bellbird. There are other records of fledgling cuckoos being fed by various birds (eg. fantail; Classified Summarised Notes, "Notornis" 22(4): 333), but they do not reliably indicate the species parasitised. The notion that chaffinches are occasional hosts apparently stems from Michie (1948), who merely saw a shining cuckoo trying to swallow a chaffinch's egg. The record for house sparrow is due to Thomson (1885), who was obviously mistaken since the egg he found in a sparrow's clutch and supposed to be a cuckoo's had pale brown spots (the cuckoo's egg is immaculate; section 10.5). The other two alleged hosts (whitehead and robin) were listed by Friedmann (1968), not all of whose references I have seen, and who relied to some extent on personal communications.

Thus, records of hosts of the shining cuckoo other than Gerygone date mostly from last century and appear to be dubious. There is an undocumented and probably unreliable record (Graham 1950) that in the 1920s shining cuckoo eggs were found in fantail-nests. Otherwise there is no recent evidence for the parasitism of any host other than the grey warbler on the mainland of New Zealand. All 16 cards for the shining cuckoo in the Nest Record Scheme (dated 1923-78) involve the grey warbler as host, as do all my records from Kaikoura. At Kowhai Bush, parasitism of six of the alleged hosts was never seen despite examination of nearly a thousand nests (mainly of robin and fantail) from 1971-78 (D. Flack, B. Lloyd, R. and M. Powlesland; pers. comm.).

9.3 MIGRATION

> "Are the seas to you as homely as our fields of curling clover?
> What old memory sends you blindly over hill and over hollow?
> Do you never doubt the way?"
>
> *The Pipiwharauroa (Shining Cuckoo)*, Eileen Duggan 1929

In contrast to their commoness in summer, shining cuckoos are rarely seen in New Zealand during May, June and July. One assumes, therefore, that they depart the country annually, and the early Maoris are said to have recognised the shining cuckoo as a migrant (Fulton 1910). From 1835 onwards, zoologists connected with New Zealand also asserted that shining cuckoos were migratory, but this was scorned by some scientists (including A.R. Wallace). As late as 1918 migration was doubted because

of the distances involved (see Fell 1947). In later years, of course, the reality of long migrations by birds was established.

Dates of arrival and departure of shining cuckoos in New Zealand, based on reports of birds first and last seen in an area were summarised by Fell (1947) and Cunningham (1953, 1955a). Dates of arrival in 1952-3 (from Cunningham 1955a) are shown in Fig. 8.1c. Early migrants are seen regularly during August and apparently land anywhere in New Zealand. The main migration, however, is in the second half of September and first half of October, and an arrival mostly in the N is suggested. Most shining cuckoos leave New Zealand by late March; some leave in April.

Fell (1947) gave four apparently reliable reports of shining cuckoos in New Zealand in May or June; Cunningham (1955a) gave a record for July; MacDonald (1955) reported a cuckoo in late May; and there are four winter-records in the Classified Summarised Notes of "Notornis" - early May, late May, early June and late July. All localities were in the North Island. Fell suggested that most non- or late-migrant shining cuckoos in New Zealand may be birds in their first calendar year. The first cuckoos of the season were seen or heard at Kowhai Bush on 8.x.1976, 29.ix.1977* and 4.x .1978*, and the last records were 16.iii.1977* and 13.iii.1978* (no record for autumn 1979; * = R. Powlesland, pers. comm.).

In November 1978, I saw an adult shining cuckoo at Kowhai Bush marked with a metal band on its left leg and a red colour-band on its right. Presumably, this was B-40201, which I banded as a nestling, and which fledged on 20.xii.1976. Apart from 11 nestling cuckoos which I banded at Kowhai Bush (three in 1976/77; four in both 1977/78 and 1978/79), only nine shining cuckoos have been banded with colours in New Zealand (all by Ecology Division, DSIR, in the Orongorongo Valley near Wellington, between 1969 and 1972). Metal on the left, red on the right was used once by Ecology Division, but they used thick (PVC "wrap-around") colour-bands.

The record suggests that shining cuckoos return to breed in their natal area. The places where I saw the cuckoo (Fig. 12.1) were 0.8-1.2 km from the nest from which it fledged two years before. In the Orongorongo Valley a shining cuckoo (B-21843) caught and banded on 18.xii.1970 was recaptured 90 m away on 10.x.1971 (A.H. Whitaker, pers. comm.). There is no proof that either bird ever left New Zealand, but if they did, then return to a previously frequented area may be the rule. Old birds of *Cuculus canorus* tend to return to the same European locality inhabited in previous breeding-seasons, and birds banded as nestlings tend to return

to the general vicinity of their natal site (Seel 1977). However, young of Cuculus canorus are rarely recovered within 6 km of their birth-place, though there is a record of Cacomantis pyrrhophanus homing to within 2 km of its natal area (Payne 1977). It makes sense that a migratory bird should improve its chances on the return-journey by homing to its first-frequented area.

10. EGGS

10.1 LAYING

I did not see shining cuckoos lay, but of six nests examined within a few hours of laying, none was damaged. There is circumstantial evidence (collated by Friedmann 1968 and Harrison 1969c) that Australian glossy cuckoos lay their egg on the ground and carry it in the mandibles to a host's nest (including *Gerygone*) for indirect deposition through the entrance. Fulton (1910) considered this method "almost certainly" employed by shining cuckoos, and Andersen (1926) quoted a manuscript alleging that it was seen often by early Maoris. Harrison (1969c) doubted that deposition by this means occurs. I tried fitting a cuckoo's egg, narrow end first, between the mandibles of a recently dead shining cuckoo. The upper mandible's lower edge followed the curve of the egg perfectly (Plate 3), and the lower mandible pressed from below such that the tension in the muscles from rigor mortis was sufficient to hold the (empty) egg in place. The cuckoo's broad bill would advantage the bird in carrying an egg, whether its own or a passerine's. In Australia, *Ch. basalis* and *Ch. lucidus* have been seen carrying eggs of *Gerygone* and *Acanthiza* (respectively) away from nests (Grant 1965, Morris and Catchpole 1978).

All 14 parasitised clutches in this study contained a single cuckoo's egg, a nearly universal phenomenon among cuckoos, presumably

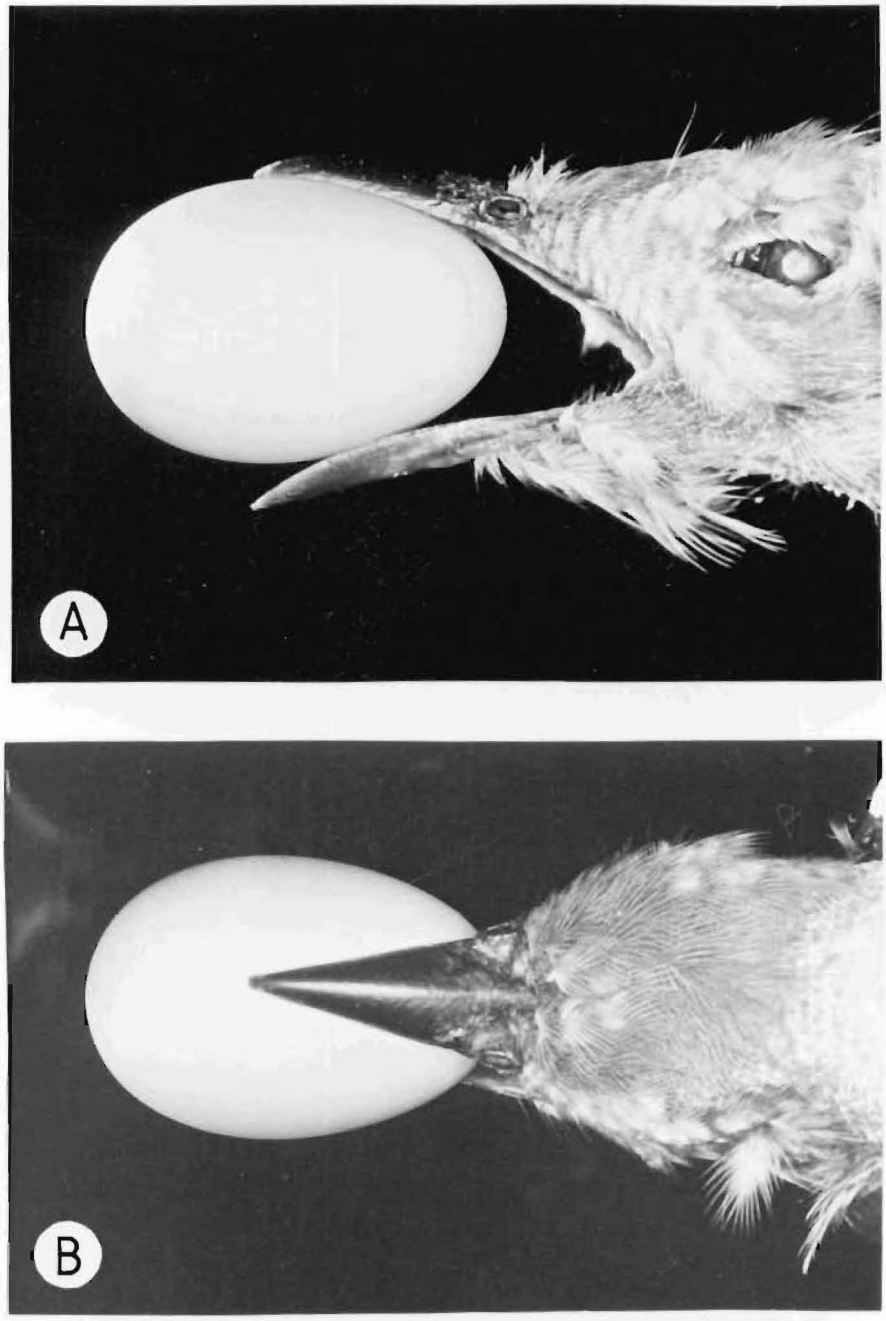

Plate 3 - A cuckoo's egg between the mandibles of a dead adult, showing the good fit. (A) Lateral view. (B) Dorsal view. (Photos: T.P. Williams.)

because the hosts can raise only one parasite (Lack 1968: 85). In terms of weight and the visits it received from the foster-parents, a nestling shining cuckoo was indeed equivalent to a brood of warblers (section 12.6). The shining cuckoo presumably removed a warbler-egg at the time of laying: in all of eight cases a nest with x warbler-eggs one day held x-1 warbler-eggs plus a cuckoo's the next. The prior marking of eggs in three warbler-clutches of four showed that the egg removed by the cuckoos varied. In one clutch the first egg laid by the warbler was removed, in another the second was removed (but the first had previously disappeared) and in another the fourth egg was replaced.

Removal of a host's egg by the adult brood-parasite at the time of laying is established for several genera (eg. *Cuculus* and *Clamator*; Friedmann 1968). It is also known for five glossy cuckoos - *Ch. lucidus, basalis, klaas, caprius* and *cupreus* (Friedmann 1968, Brosset 1976) - and is inferred in four others. The phenomenon may encourage acceptance by the host of the altered clutch, the size of which is perhaps sensed via the brood-patch (Hamilton and Orians 1965).

A female cuckoo collected in Christchurch on 6.xi.1977 had about a third of an almost intact egg-shell in its gizzard. The egg was not a cuckoo's (it was speckled), but may have been a warbler's. November is the main month of laying by cuckoos (section 10.2), and the observation suggests that warbler-eggs removed during parasitism or at other times, are swallowed. Morris and Catchpole (1978) witnessed the ingestion by *Ch. lucidus* of an egg belonging to its host, but the shell was discarded.

Many passerines have anti-parasite adaptations - they may abandon the parasitised nest, remove the parasite's egg, or bury the entire clutch beneath fresh nesting material and then re-lay (Rothstein 1975). However, I saw no evidence of such behaviour during the present study. This is not surprising because the ability of the host to discriminate alien eggs probably evolves in parallel with the extent of the parasite's egg-mimicry (Lack 1963), and the latter is non-existent in the shining cuckoo (section 10.5).

10.2 DATES OF LAYING

At Kowhai Bush I obtained the laying-dates of 22 cuckoo-eggs, either directly in the course of daily visits to nests, or by estimation - working back from known dates of hatching and fledging using the average incubation and nestling periods (sections 10.6, 11.3), or by ageing a

nestling from its weight and measurements (Table 11.2). The 16 shining cuckoo cards in the Nest Record Scheme yielded nine dates of laying, hatching or fledging (1923-67) from which I calculated the full series.

Fig. 10.1 shows that shining cuckoos laid from mid-October (earliest egg 14.x.1978; Kowhai Bush) until the third quarter of December (latest egg 16.xii.1976; Kowhai Bush) or early January (latest egg 1.i.1924; Nest Record Scheme). Thus the laying-season was 10 weeks at Kowhai Bush and 12 weeks for New Zealand as a whole. The modal week of laying was the third or fourth quarter of November. Two adult female cuckoos which I dissected each had a full-sized egg in the oviduct ready to be laid. One bird died on 28.xi.1968, and the other during the second week of December 1975.

Cuckoos apparently laid successively earlier from 1976 to 1978. Data for the first year may have reflected my initial inexperience at finding late nests, while I regard the record for mid-October 1978 as exceptional, since it was 2-3 weeks earlier than any previous record. However, there was a second record of early laying that year. On 6.xi.1978 I found an abandoned nest containing a single cuckoo-egg which was presumably laid in mid-October or earlier, since it was almost completely dehydrated. Excepting these two records, the cuckoo parasitised only the warbler's late clutches, ie. those initiated on or after 23 October (section 5.2). Clutches produced by warblers in mid-October probably represented re-laying after loss of a first clutch (Fig. 5.1), so it remains unlikely that first clutches are ever parasitised.

Similarly, in south-western Australia first or early clutches of *Acanthiza chrysorrhoa* usually escape parasitism by *Ch. lucidus plagosus*. The Australian race may lay earlier than the shining cuckoo - as early as late August (Ford 1963).

Payne (1973) determined the pattern of laying of African *Chrysococcyx* from ovarian histology. Individual females lay on alternate days, in series or clutches of about three, with delays of several days between series. A similar pattern is likely in the shining cuckoo.

10.3 TIME OF LAYING RELATIVE TO THE HOST'S CYCLE

Five (possibly six) cuckoo-eggs in a sample of seven were laid after completion of the warbler's clutch (Fig. 10.2). At the extremes, one was laid on the same day as the warbler's penultimate egg, and another was laid after the warbler's clutch had been incubated 7-10 days. It is

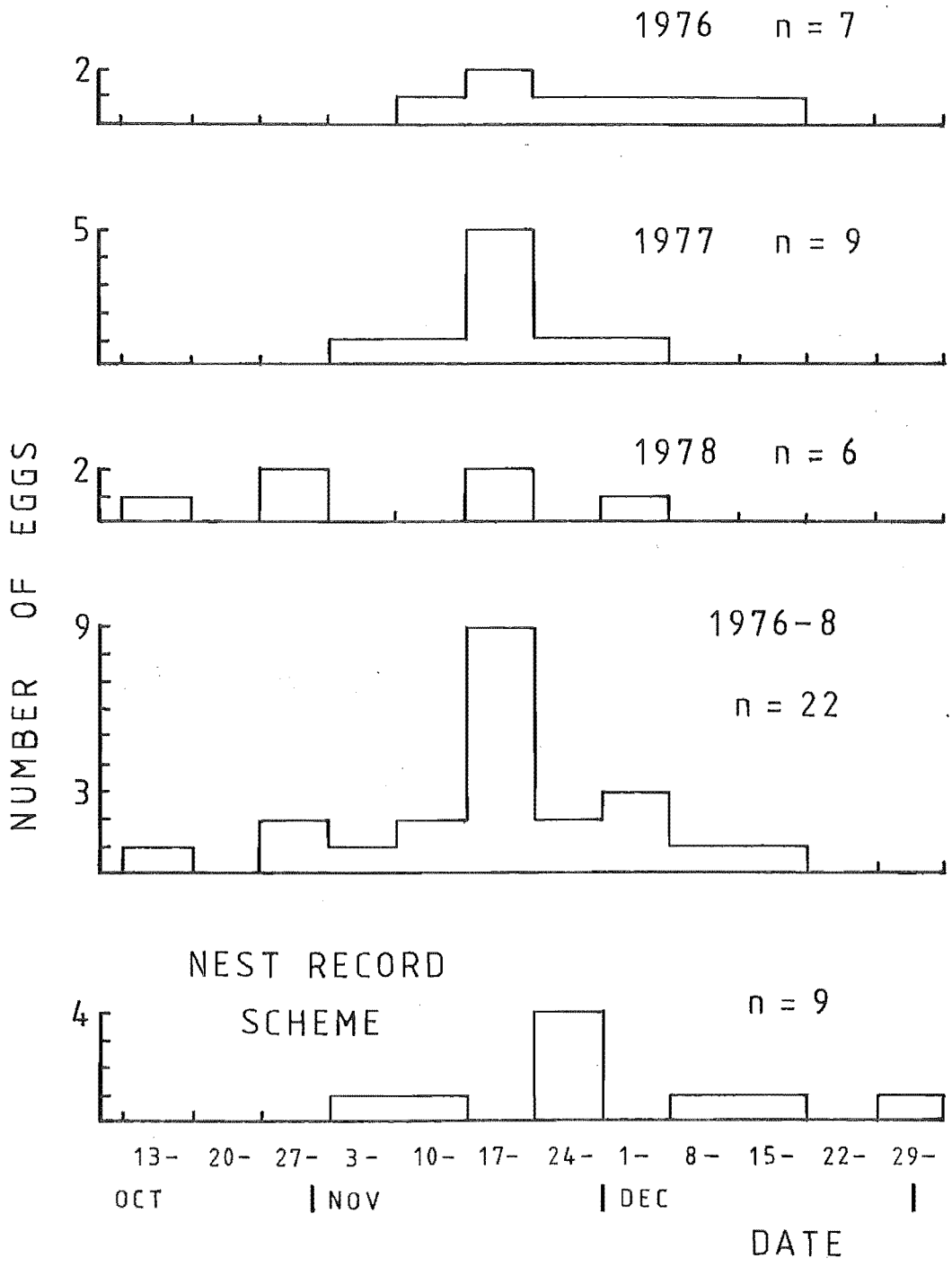

Figure 10.1 - Dates of laying of cuckoo-eggs (Kowhai Bush and Nest Record Scheme), grouped into weeks.

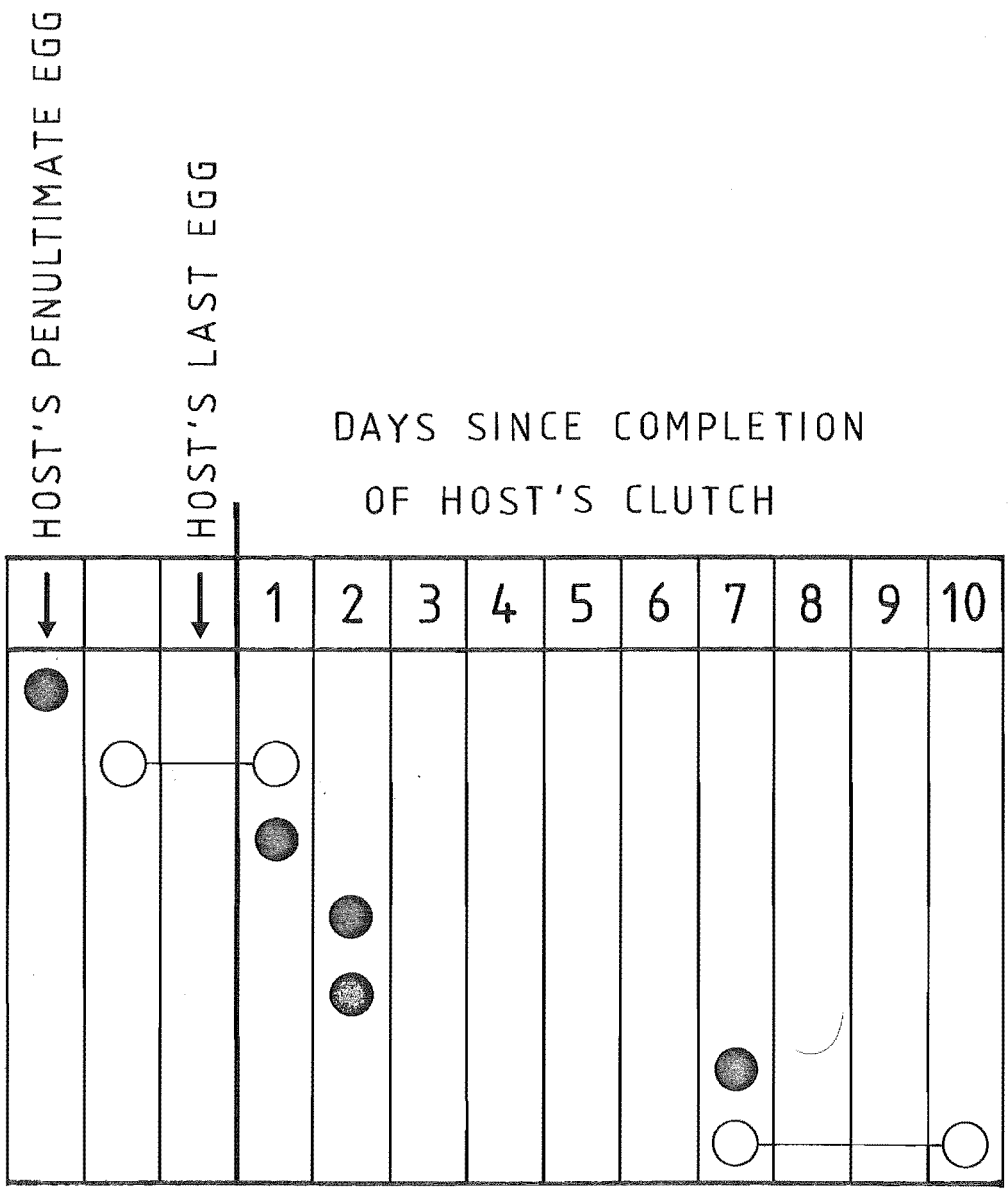

Figure 10.2 - Days on which shining cuckoos laid, in relation to the host's laying-cycle (open circles = exact day unknown).

obviously advantageous for a cuckoo to lay at about the time the host begins incubating so that the parasite hatches early (by virtue of its short incubation period; section 10.6), evicts the host's eggs, and receives all the food that the foster-parents deliver. That some shining cuckoos laid a week into the warbler's incubation period suggests that there may be difficulties in finding nests suitable for parasitism. In an eighth instance I found an abandoned nest containing a single warbler's egg, at least a week old to judge from its weight. The next day the nest held a single cuckoo's egg - further proof of laying that was poorly synchronised to that of the host, and an indication that cuckoos will parasitise a clutch of one.

Gaston (1976) found that Indian pied crested cuckoos (*Clamator jacobinus*) laid during or after egg-laying by the hosts (babblers, *Turdoides* spp.). The latter suggested inefficiency or a preference for parasitising the correct host at a less appropriate time, rather than a wrong host at the right time. *Cuculus canorus* only exceptionally lays after the host starts incubating (Chance 1922). The commonest and most-studied southern African cuckoo (the didric, *Chrysococcyx caprius*) usually lays during the host's laying-period - rarely before, though "not infrequently" after (Jensen and Jensen 1969). *Ch. lucidus plagosus* deposits its egg before, during or after laying by the host (Ford 1963). Thus the shining cuckoo is perhaps unusual in regularly laying after completion of the host's clutch.

10.4 FREQUENCY OF PARASITISM

In this analysis I considered only late nests, and excluded the two exceptionally early records of parasitism (section 10.2). My criteria for deciding that a late nest had not been parasitised were that:

a. I had followed it during laying and the first half of incubation, without noting parasitism, or
b. it contained four nestling warblers, or four warbler-eggs close to hatching.

A nest satisfying the second criterion could have been parasitised only in the unlikely event that it received five warbler-eggs, one of which was replaced by a cuckoo-egg which was somehow lost.

There were 14 nests in 1976/77, 18 in 1977/78 and 8 in 1978/79, that I examined and which were available for parasitism. Of these, eight, nine and five (respectively) were parasitised, giving frequencies

of parasitism of 0.57, 0.50 and 0.63 (0.55 in total , n = 40). Of 61 late warbler-nests reported to the Nest Record Scheme, 14 were parasitised and 19 were definitely not, so that the frequency of parasitism was 0.42. Pooling all data, 49% of late nests were parasitised (n = 73).

These frequencies of parasitism are relatively high. Brosset (1976) found that *Chrysococcyx cupreus* in Gabon parasitised only eight of 600 theoretically available nests. Parasitism by the black cuckoo (*Cuculus clamosus*) and Klaas's cuckoo (*Ch. klaas*) in South-West Africa varied with year and location but never exceeded 40% of available nests (Jensen and Clinning 1974). The average frequency of parasitism of the nine cuckoos common in southern Africa was less than 3% (Payne 1977); the same as for *C. canorus* parasitising song-birds in England (Lack 1963), except that in specific local instances frequencies of parasitism for the latter reached 56%. In Cambridgeshire *C. canorus* parasitised 21% of nests of *Acrocephalus scirpaceus* (Wyllie 1975). Near Canberra, *Ch. lucidus plagosus* parasitised only 3.4% of nests of *Malurus cyaneus* (Rowley 1965), but the latter is not the cuckoo's main host.

At Kowhai Bush frequencies of parasitism were 0.85 in Habitat 1 (n = 13) and 0.30 in Habitat 2 (n = 10). It could be that in the open forest of Habitat 1 cuckoos more easily found nests by following the owners (as I did), but the samples are small.

10.5 COLOUR, SHAPE, MEASUREMENTS AND WEIGHT

Oliver's description (1955), repeated in the Field Guide (Falla *et al.* 1970), and traceable to Buller (1888), that eggs of the shining cuckoo are "greenish or bluish white to olive brown or dark greenish brown", lacks clarity. The 16 eggs I saw at Kowhai Bush (shells from six collected) were olive-green. On close examination they seemed to have a base-colour of pale grey-green, overlaid with a finely mottled or granular olivaceous pigment. This superficial colouring varied in intensity so that some eggs were darker than others. Serventy and Whittell (1951: 251) reported the olivaceous pigment to be water-soluble in *Ch. lucidus plagosus*, and my own trial with fragments of shell suggested likewise for the shining cuckoo. Some eggs apparently lost patches of the superficial pigment after rubbing against warbler-eggs in a parasitised clutch.

Eggs of the shining cuckoo do not mimic the host's (described in section 5.5: see Plate 6A). My evidence also suggests that they are

monomorphic (a characteristic of Australasian *Chrysococcyx*; Friedmann 1968).

Marchant (1972) suggested that *Ch. lucidus plagosus* lacks egg-mimicry because the nests of its host (*Acanthiza chrysorrhoa*) are dark inside. By contrast, *Ch. basalis* in Australia has mimetic (though monomorphic) eggs and hosts with nests less enclosed than those of *A. chrysorrhoa*. Most warbler-nests at Kowhai Bush were dark inside, and many were constructed such that I needed a dental mirror to view the contents. The implication of the absence of egg-mimicry in the shining cuckoo is that it encounters no antiparasite adaptations, perhaps because the warbler cannot clearly see the clutch in the darkened nest.

The grey warbler's egg is oval, with one end narrower and more pointed than the other, while the cuckoo's egg is typically almost elliptical, with the smaller end nearly as blunt as the larger. On average four cuckoo-eggs from Kowhai Bush were 18.68 mm long and 12.63 mm wide (Table 5.3), that is, slightly larger than the average for warbler-eggs. However, the ranges for length, width and volume-index in the two species overlapped. The smallest cuckoo-egg (17.3 x 12.0 mm) was unusual in being the same oval shape as a warbler's. According to Schönwetter (1964), eggs of the shining cuckoo are 18.0-20.3 mm long and 12.5-15.2 mm wide (mean: 18.9 x 13.1 mm).

Two shining cuckoo eggs on the day they were laid weighed 1.8 g, and two others 0-4 and greater than five days old were 1.9 g. Thus, fresh eggs were 1.85 g on average or 0.4 g heavier than those of the warbler (section 5.5). According to Schönwetter (1964), the shining cuckoo's egg weighs 1.73 g, and that of *Ch. lucidus plagosus* 1.66 g.

Adult shining cuckoos weigh 23.1 g (section 9.1), so (using my data) the fresh egg is 8.0% of the adult's body-weight. This value is 7.9% in *Ch. lucidus plagosus*, and 6.2% in the larger *Ch. caprius* (41 g; Schönwetter 1964). Most parasitic cuckoos, with obvious advantage for successful parasitism, have smaller eggs than are laid by most birds of similar size. At one extreme *Cuculus canorus* parasitises passerines much smaller than itself and lays eggs only 2.4% of its body-weight (Lack 1968: 86). The opposite extreme for cuckoos (eggs about 8% of body-weight) is achieved in large cuckoos parasitising large hosts (eg. *Clamator glandarius*; Lack 1968), or in small cuckoos parasitising small hosts (eg. the shining cuckoo) where less severe reduction of eggs is required.

10.6 INCUBATION PERIOD

I took the incubation period of a cuckoo-egg to be the interval in whole days from the day it appeared in the nest (day 1) up to and including the day before the nestling was seen (error ± 24 hours). The mean incubation period of three eggs was 15.5 days, but the interval varied with the time of laying relative to the host's cycle. One egg laid coincident with the warbler's penultimate egg was not immediately incubated, and took 17 days to hatch. Another egg laid shortly after the host began incubating, hatched after 16 days, and an egg deposited a week into the host's incubation period hatched in only 13 or 14 days. Each interval is less than the host's average incubation period (19.5 days; section 5.8), but the longest approaches the host's minimum (17.3 days).

Cuckoos have some of the shortest apparent incubation periods on record, and some retain the egg and incubate it within their body for about a day before laying (Perrins 1967, Lack 1968: 88). A short incubation period allows the cuckoo to hatch before the host's eggs hatch, or soon after. Thus the nestling cuckoo either evicts eggs, and receives all the food brought by the foster-parents, or it evicts foster-siblings while they are small, so minimising competition for food.

Incubation periods of other glossy cuckoos are poorly known: *Chrysococcyx klaas* and *caprius* - 11-12 days (Jensen and Jensen 1969, Jensen and Clinning 1974); *Ch. cupreus* - up to 13 days (Brosset 1976); *Ch. lucidus plagosus* - probably about 13 days (Courtney and Marchant 1971). Parasitic cuckoos usually have incubation periods of 11-14 days; often 2-4 days shorter than those of their hosts (Payne 1977). The shining cuckoo's incubation period is relatively long, but the warbler's is also longer than usual (section 5.8), and an average difference between them of four days is maintained.

11. NESTLINGS AND JUVENILES

11.1 DATES OF HATCHING AND FLEDGING

The dates of hatching and fledging of nestling cuckoos at Kowhai Bush, and as reported to the Nest Record Scheme, are shown as histograms (Figs 11.1 and 11.2), with observed, estimated and hypothetical dates combined (see section 6.2). Cuckoos hatched from late October (earliest hatchling 29.x.1978; Kowhai Bush) to the second quarter of January (latest hatchling 17.i.1924; Nest Record Scheme). They fledged from the third quarter of November (19.xi.1978; Kowhai Bush) to early February (5.ii.1924; Nest Record Scheme). The modal times of hatching and fledging were early and late December respectively. The earliest record of hatching/fledging at Kowhai Bush was probably unusual (see section 10.2), although there are exceptional records in the Classified Summarised Notes of fledglings in early November ("Notornis" 19 (supplement): 67) and in early March ("Notornis" 2(7): 170).

11.2 EVICTION

The young of cuckoos which parasitise hosts much smaller than themselves require all the food that their foster-parents bring, and so must destroy any of the host's nestlings. The nestlings of many species of cuckoo achieve this by pushing eggs or other young out of the nest soon after hatching. Eviction is well-known in *Cuculus* (Lack 1968: 88), and has been reported in about half the glossy cuckoos (Friedmann 1968). Nestling shining cuckoos evicted the nest's contents in all eight cases during my study.

The instances of eviction are given in Table 11.1. Cuckoos usually hatched before any warblers, but there were exceptions since some cuckoos laid well after the host began incubating (Fig. 10.2). Eviction occurred when cuckoos were 3-7 days old ($\bar{x}$ = 4 days; day of hatching = day 0), and in three cases eviction apparently took two days. Both eggs and nestlings were evicted. On the day of eviction seven nests held at least one nestling warbler, so that a brief period of inter-specific competition for food was common.

Cuculus canorus evicts when between 10 hours and 4 days old (Welty 1975). Nestlings of *Ch. caprius* are 1-5 days old (day of hatching = day 0) when they perform eviction (Jensen and Jensen 1969), and they evict nestlings in preference to eggs, either because eggs are harder to evict,

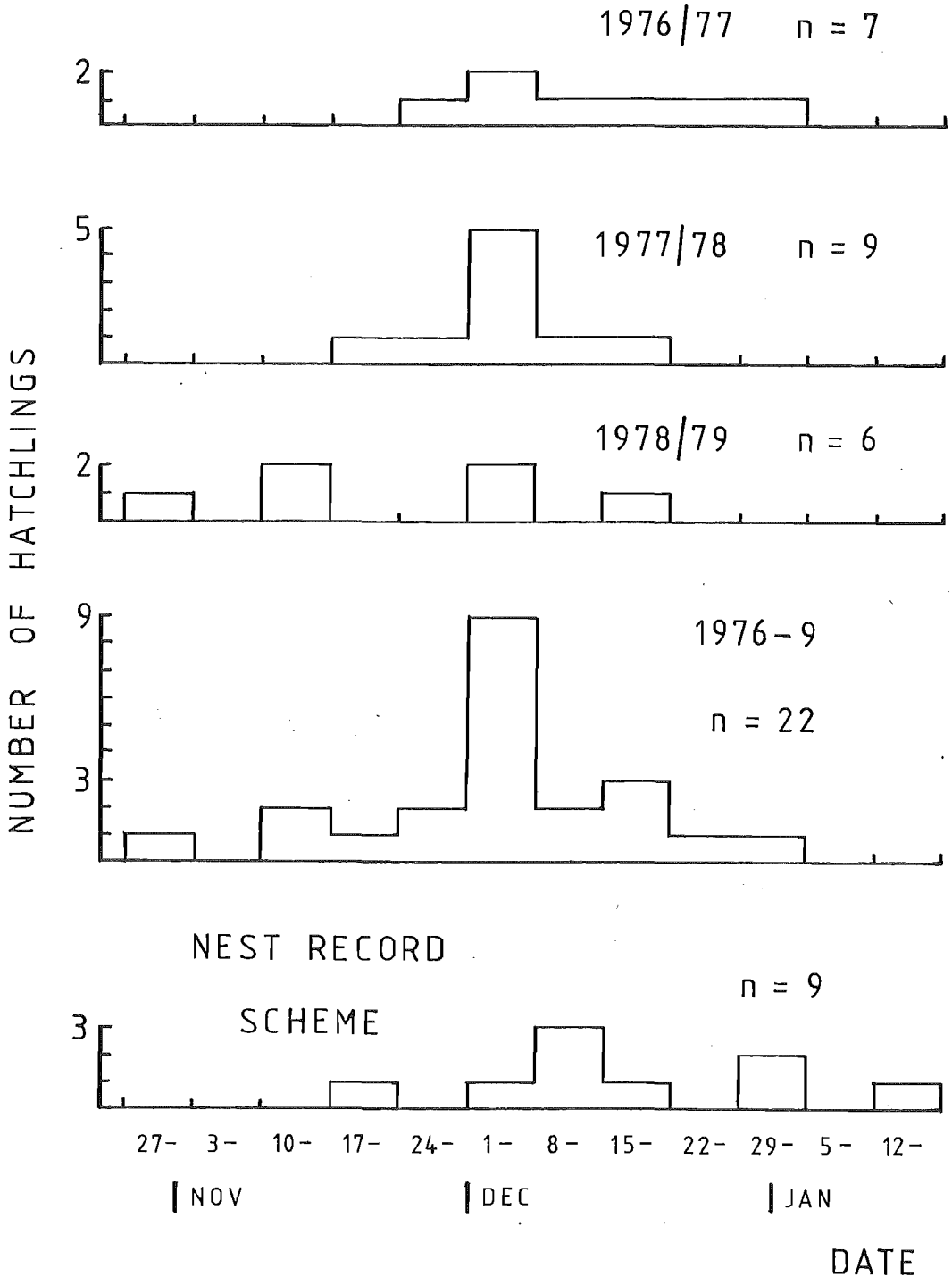

Figure 11.1 - Dates of hatching of cuckoos (Kowhai Bush and Nest Record Scheme), grouped into weeks.

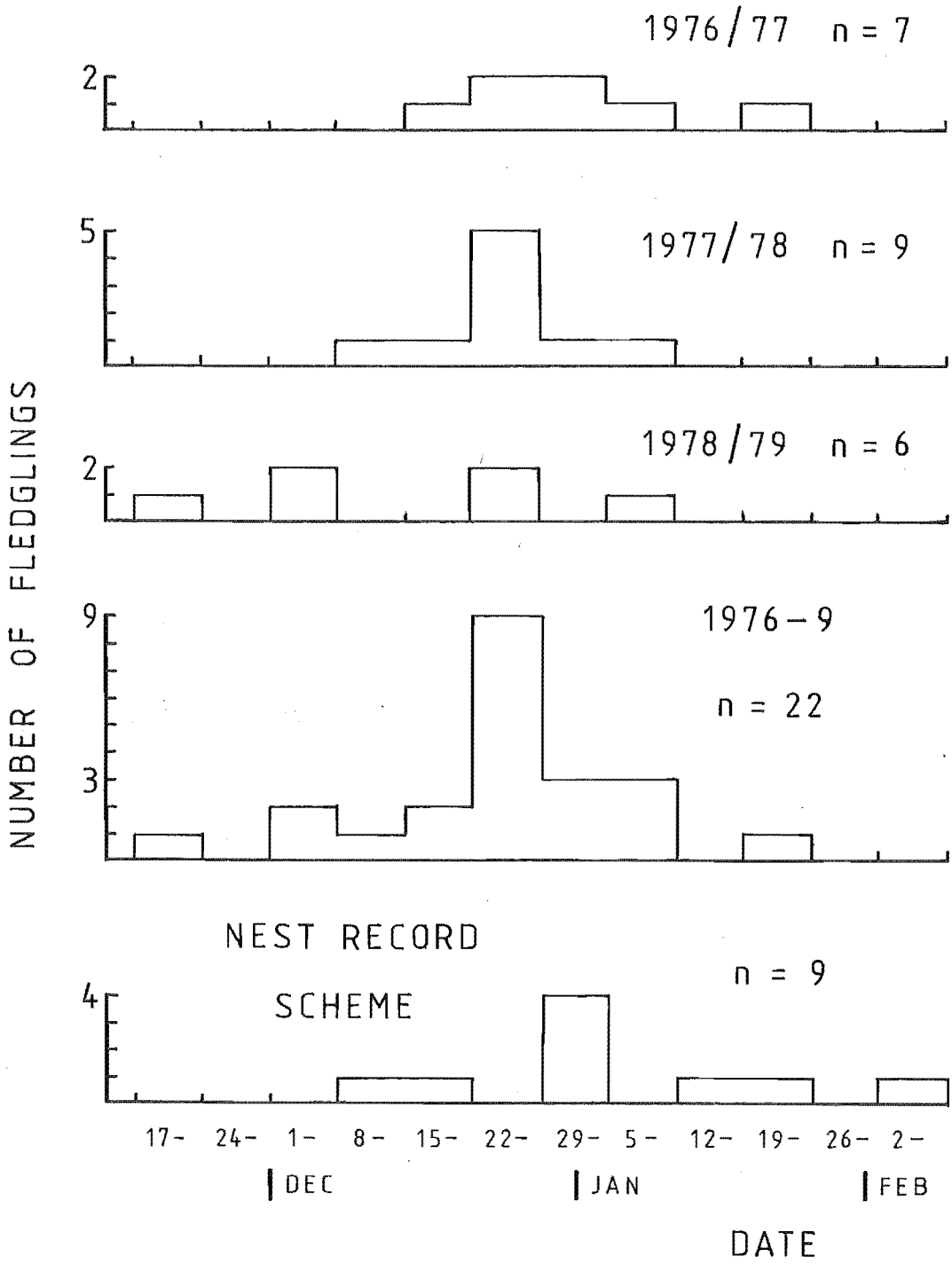

Figure 11.2 - Dates of fledging of cuckóos (Kowhai Bush and Nest Record Scheme), grouped into weeks.

Table 11.1 - Instances of eviction showing other contents of the nest when the cuckoo hatched, contents evicted by the cuckoo, and the cuckoo's age at eviction (e = egg, n = nestling).

nest-contents when cuckoo hatched	contents evicted by cuckoo	age (days) of evicting cuckoo
1e	1e	3
3e	2e, 1n	3
3e	1e, 1n*	3
3e	1e, 2n	3-4
3e	1e, 2n	3-4
3n	3n	3-4
3e	3n	5
1n	1n	7

* one egg disappeared

or because nestlings present a greater stimulus (Jensen and Vernon 1970). *Ch. cupreus* evicts nestlings but not eggs (Brosset 1976). That glossy cuckoos encounter difficulties with eviction is not surprising since they largely parasitise species with enclosed nests. The shining cuckoo must raise objects about 4 cm (Appendix 2) to evict them, and must thrust in only one direction. At one nest a nestling warbler was pushed through a small hole in the wall of the nest where it had lodged and died. Otherwise all evicted contents dropped to the ground directly below the entrance or caught on intervening vegetation.

Nestlings of *Cuculus* have a sensitive concave back with which they push objects out of the nest (Lack 1968, Payne 1977), whereas in *Chrysococcyx caprius* the nestling's back is flat (Jensen and Vernon 1970). The nestling shining cuckoo has a large flat back (about 2.5 cm^2 at five days old) and bilaterally paired spinal pterylae with a median dorsal apterium. The latter may facilitate eviction, since it tends to make the dorsum concave. Nestling warblers (as with most passerines) have a convex dorsum and a median spinal pteryla. It may also be significant that cuckoos grip the nest soon after hatching (whereas warblers do not), and that they hold the wings out stiffly until 7-8 days old.

One example of eviction, where a cuckoo hatched three days after the single warbler which shared the nest, is noteworthy (Fig. 11.3). The warbler was heavier than the cuckoo, and successfully competed with it for 6½ days, by which time the cuckoo reached the warbler's weight and evicted it (warbler 9½ days old). The cuckoo's growth-rate accelerated as soon as the bird was free of competition. At 6 days old the cuckoo weighed 5 g compared with the normal average of 8 g (Fig. 11.4). This demonstrates the inefficient result of late laying by cuckoos (section 10.3) - in this instance the female laid 7 days after the host began incubating.

11.3 NESTLING PERIOD

I took nestling period as the interval in whole days from the day I first saw the nestling cuckoo (day 1) to the midnight before it was first absent from the nest. The nestling period was 19 days in each of three cases. Five other nestlings with unknown dates of hatching, but which I tentatively aged from their weights and measurements, apparently took 19-22 days to fledge ($\bar{x}$ = 21 days). Thus the parasite's nestling period was longer than the average for the warbler's own young (17 days; section 6.4). The cuckoo's nestling period is probably more plastic than the warbler's since it may be lengthened by initial inter-specific competition.

Nestling periods of glossy cuckoos are even more poorly known than incubation periods: *Chrysococcyx klaas* - 15-21 days (Jensen and Clinning 1974); *Ch. caprius* - about 20 days (Jensen and Jensen 1969); *Ch. lucidus plagosus* - about 19 days (Courtney and Marchant 1971).

11.4 GROWTH

Once daily in all three years I weighed cuckoos and measured their right tarsus and total culmen (defined in section 6.6). Introductory remarks in sections 6.5 and 6.6 apply here. The average weights and measurements of cuckoos for each day of the nestling period are given (Table 11.2) for their value in ageing, and the data are plotted in Fig. 11.4.

The weights of nestling cuckoos increased sigmoidally with age. The maximum average weight was 22.2 g, on day 16, and there was only a slight recession in weight before fledging. The heaviest nestling was 23.2 g, which is close to the mean weight of adults (23.1 g; section 9.1). Thus adult weight approximates the asymptote which the weight of nestlings approaches but generally does not exceed. This

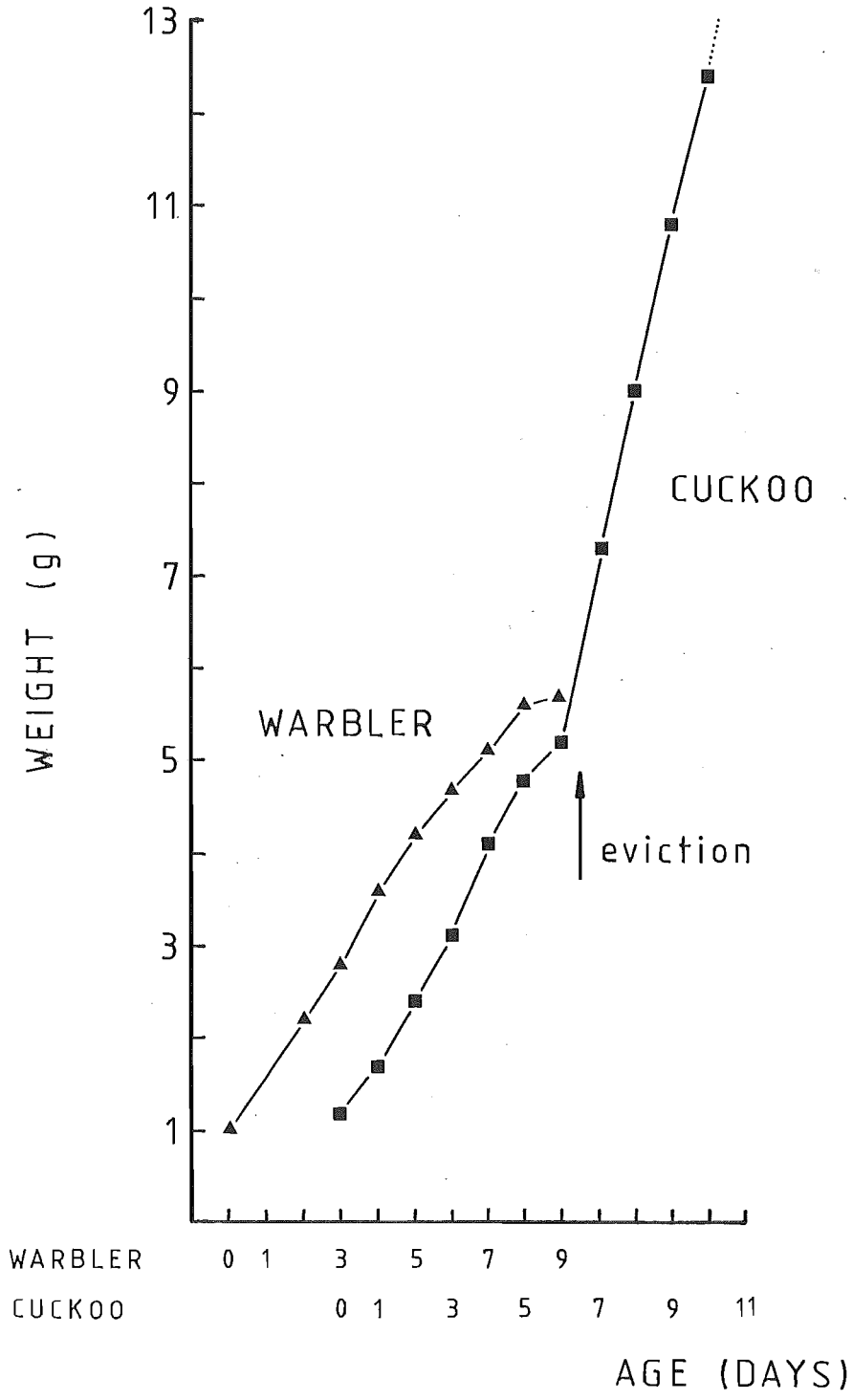

Figure 11.3 - Daily changes in weight of a warbler and cuckoo which shared a nest, showing the effect of inter-specific competition on the parasite's growth.

Table 11.2 - Weights (g) and linear measurements (mm) of nestling shining cuckoos; day 0 = day of hatching.

	weight				tarsus				culmen			
age	$\bar{x}$	n	s	range	$\bar{x}$	n	s	range	$\bar{x}$	n	s	range
0	1.60	7	0.22	1.2 - 1.9	7.26	7	0.43	6.6 - 7.7	5.87	7	0.22	5.5 - 6.1
1	2.24	7	0.29	1.7 - 2.6	8.30	7	0.35	7.6 - 8.6	6.31	7	0.15	6.1 - 6.5
2	3.09	7	0.43	2.4 - 3.7	9.49	7	0.49	8.8 - 10.3	7.10	7	0.33	6.7 - 7.7
3	4.38	6	0.66	3.1 - 4.9	10.54	7	0.55	9.8 - 11.2	7.79	7	0.39	7.2 - 8.2
4	5.25	4	1.84	3.3 - 7.1	11.55	4	0.93	10.4 - 12.4	8.48	4	0.53	7.8 - 8.9
5	6.58	6	1.51	4.5 - 7.7	12.52	6	0.96	11.4 - 13.9	9.15	6	0.57	8.4 - 9.8
6	7.82	6	1.82	5.2 - 9.2	13.23	6	1.09	11.8 - 14.5	9.80	6	0.78	8.7 - 10.6
7	9.62	6	1.75	7.3 - 11.3	14.08	6	1.00	12.7 - 15.6	10.42	6	0.81	9.3 - 11.1
8	11.80	3	2.46	9.0 - 13.6	15.50	3	0.89	14.5 - 16.2	11.20	3	0.87	10.2 - 11.8
9	12.78	4	1.90	10.8 - 14.5	15.55	4	0.58	15.0 - 16.3	11.48	4	0.75	10.7 - 12.3
10	15.40	5	2.45	12.4 - 17.4	16.50	5	0.90	15.1 - 17.4	12.40	5	0.89	11.4 - 13.4
11	17.28	5	2.04	14.9 - 18.9	17.78	4	0.79	16.7 - 18.6	13.10	4	0.64	12.2 - 13.7
12	18.46	5	1.89	15.9 - 20.1	18.18	5	0.74	17.4 - 19.0	13.08	4	0.70	12.5 - 13.9
13	19.78	4	1.47	17.9 - 21.0	18.38	4	0.87	17.7 - 19.6	13.57	3	0.40	13.2 - 14.0
14	21.00	4	0.72	20.3 - 22.0	19.10	4	0.61	18.5 - 19.8	14.13	3	0.40	13.7 - 14.5
15	21.58	4	1.08	20.6 - 23.0	19.63	4	0.28	19.3 - 19.9	14.50	3	0.27	14.3 - 14.8
16	22.15	4	0.37	21.8 - 22.6	20.18	4	0.22	19.9 - 20.4	14.90	3	0.56	14.3 - 15.4
17	21.97	3	1.07	21.3 - 23.2	20.93	3	0.32	20.7 - 21.3	15.90	2	0.42	15.6 - 16.2
18	21.73	3	1.32	20.3 - 22.9	21.23	3	0.40	20.8 - 21.6	15.90	2	0.14	15.8 - 16.0

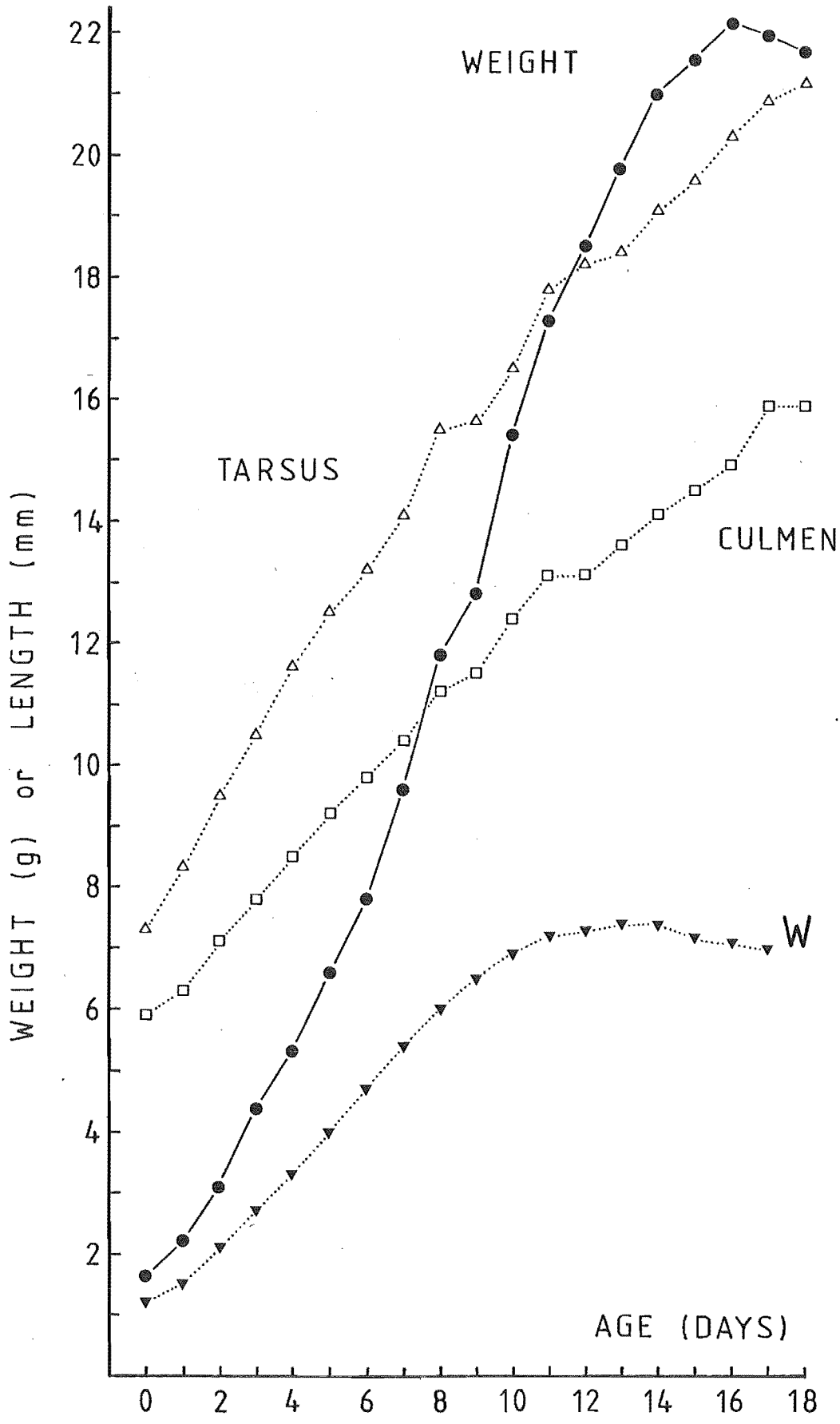

Figure 11.4 - Average weights and measurements of nestling cuckoos as a function of age (see Table 11.2). W = average weight-age-curve of individual nestling warblers (all brood-sizes).

pattern of growth in weight is probably typical of altricial birds, certainly of most passerines (see Ricklefs 1968a). The linear regression of weight on age ($y = 1.33x + 0.89$) fits well ($r^2 = 0.94$) and is significantly linear (F-test; $P < 0.01$).

The weight at hatching of cuckoos (about 1.2 g; Appendix 4) was 5.5% of the average weight of nestlings on the day before fledging (21.8 g). *Cuculus canorus* hatches at 3.6 g or 4.1% of its final weight (87 g; Lack 1947). Thus both the egg of the shining cuckoo in relation to adult weight (section 10.5), and the newly-hatched nestling in relation to the pre-fledgling, are slightly heavier than in *Cuculus canorus*. The average weight of cuckoos on day 0 (1.6 g; Table 11.2) was close to that of warblers (1.2 g; Table 6.5), but the ratio of maximum average nestling-weights (22.2 g : 7.4 g) was 3 : 1. The enormous capacity for growth of the cuckoo compared with the single warbler (Fig. 11.4) was expressed in average changes in weight of up to 2.6 g/day. In just 16 days shining cuckoos increased to 19 times their weight at hatching. Fifty-fold increases are known in other cuckoos (Welty 1975).

The linear regressions of tarsal length and culmen-length on age fit well ($r^2 = 0.96$ and 0.97 respectively) and are significantly linear (F-test; $P < 0.01$). The equations, $y = 0.80x + 8.09$ and $y = 0.59x + 6.06$ (respectively), confirm the steeper slope and greater y-intercept for tarsus (Fig. 11.4).

The mean weight of eight nestlings on the day before fledging was 21.8 g ($s = 1.39$), or 94.5% of adult weight ($\bar{x} = 23.1$ g). Similarly, the average tarsal length of nine incipient fledglings was 21.5 mm ($s = 0.52$), or 98.8% of tarsal length in adults ($\bar{x} = 21.8$ mm, $n = 19$, $s = 0.58$). Cuckoos fledged with wings 60-65 mm long, compared with an average length of 102.5 mm in 19 adults. Tails were 30-35 mm long at fledging, and 71.1 mm as an average for 16 adults. Thus the long nestling period produces highly advanced fledglings in terms of adult size, but a considerable development of plumage is apparently completed in juveniles.

11.5 BROODING AND SANITATION

Nestling cuckoos, as with young warblers (section 6.8), were brooded only by the female warbler, but fed by both sexes. Brooding by the warbler of either one species or the other, individuals of which

differ in their number, size and time in the nest, constitutes a natural experiment in exogenous influences on a pattern of behaviour. In 1977/78 and 1978/79 I watched brooding of cuckoos for 23 hours in total (see section 2.2) to test the null hypothesis that single nestling cuckoos and broods of 3-4 warblers were brooded to the same extent.

The maximum age of a brooded cuckoo was 16 days (conditions sunny and warm), so cuckoos required brooding for about six days longer than warblers. As with warblers, the amount of brooding declined linearly with maturation of the young (Fig. 11.5). The line for cuckoos fits poorly (r^2 = 0.48, n = 24) but is significantly linear (F = 20.19; $P < 0.01$). The regression differs from that for warblers (variances significantly heterogeneous; χ^2 = 5.12 for 1 d.f.; $P < 0.05$), being less steep despite the same initial amount of brooding. According to the equation, time spent brooding cuckoos was nil at 18.0 days, 7.3 days later than for warblers. The average length of a brooding-spell for cuckoos was 10.2 minutes (n = 47, s = 7.73, range = 0.5-30.5 minutes), nearly double that for warblers (see section 6.8; significant difference t = 3.00 for 108 d.f.; $P < 0.01$).

I reject the null hypothesis, accepting instead that cuckoos were brooded in longer spells and for a greater portion of their nestling period than warblers. This supports the principle established by controlled experimentation, that the brooding-period is not entirely endogenous and is modified by external stimuli (Winkel and Berndt 1972, Welty 1975: 347).

On 71% of occasions (n = 53) the female warbler ceased brooding cuckoos because the male brought food, a slightly higher figure than for the brooding of warblers (section 6.8).
The longer brooding-spells for cuckoos probably meant that a male arriving at the nest with food more often found the female in attendance. As with broods of warblers, the

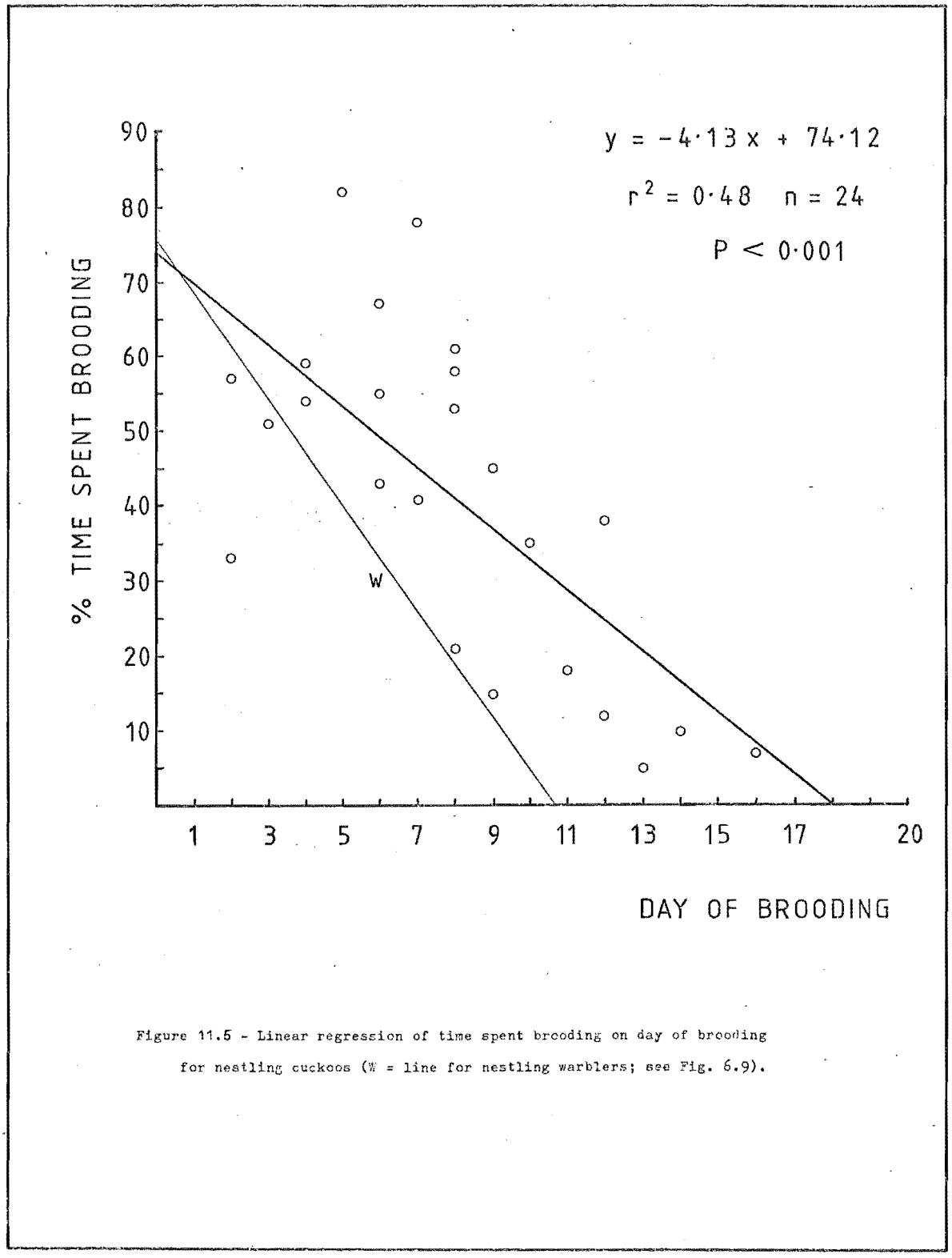

Figure 11.5 - Linear regression of time spent brooding on day of brooding for nestling cuckoos (W = line for nestling warblers; see Fig. 6.9).

average brooding-spell associated with the female leaving the nest spontaneously (13.4 minutes; n = 13, s = 8.18) was longer than when the male's interaction caused her to leave (8.5 minutes; n = 32, s = 6.77). The difference was significant ($t = 2.06$ for 43 d.f.; $P < 0.05$).

Cuckoos were longer in the nest than warblers, and took longer to develop insulative plumage (compare Appendices 3 and 4). Cuckoos may have been brooded for more days than warblers because they developed homoiothermy later. On average nestling cuckoos received fewer feeding-visits than broods of three or four warblers (section 12.6). With less effort needed to feed the parasite, the female warbler may have had time for longer brooding-spells than associated with her natural young.

Adult warblers removed faecal sacs from nests containing cuckoos in the same way as for broods of warblers (section 6.8), and I occasionally saw sacs carried to perches 6-15 m from the nest and dropped. However, warblers removed faecal sacs from cuckoos on only 14% of visits to the nest (n = 189), suggesting that one cuckoo produced fewer than a brood of 3-4 warblers (see section 6.8). There was no apparent difference between the sexes in the proportion of visits on which a faecal sac was removed (♂♂ 12%, ♀♀ 15%).

11.6 JUVENILES

> "Why, then, foolish little fledglings, do you ever seek to follow?
> What old meekness makes you follow that strange one that gave you over,
> Nor remembered you a day?"
>
> *The Pipiwharauroa (Shining Cuckoo)*, Eileen Duggan 1929

I considered cuckoos to be juveniles from their fledging until their presumed departure the following autumn.

The most obvious external feature distinguishing juveniles from adults was the pale yellowish underparts, which are white in mature birds. The iridescent green ventral barring of newly-fledged cuckoos was slightly less pronounced than in adults, but was essentially the same - the sides and flanks were strongly barred, the belly unbarred, and the breast irregularly barred (appearing almost longitudinally striped from a short distance). The dorsal plumage of juveniles lacked the deep copper sheen of adults, and the bill and tail were shorter than in adults. Juveniles had a grey bill (black in adults) with a ventral base of pink, and blue-grey legs (black in adults). Friedmann (1968) and Marchant (1972) stated that the young of Indo-Australian glossy cuckoos are not barred below. As a generalisation this clearly does not hold.

Newly-fledged cuckoos, which were weak fliers, behaved secretively, and perched silently and immobile for long periods. They were best located indirectly, by following the warblers that fed them. Later, however, when flying well, cuckoos cheeped loudly, begged vigorously by fluttering the wings, and followed the warblers, cheeping in flight. They were aggressive towards the foster-parents and often pecked at them immediately after the delivery of food.

I saw cuckoos being fed for up to 28 days after fledging, a week short of the maximum period of parental care of young warblers (section 7.2), but my data may have been incomplete. Cuckoos caught prey from about their 16th day free of the nest. For the first 3-4 days both sexes of foster-parent cared for the fledgling, but thereafter the cuckoo was nearly always the male's responsibility. Fledglings of *Chrysococcyx klaas* are fed for at least 25 days (Jensen and Clinning 1974), and those of *Ch. caprius* for up to 38 days (Reed 1968).

A juvenile shining cuckoo collected in Christchurch on 12.ii.1979 had a layer of sub-cutaneous fat several millimetres thick on the lower abdomen, and other deposits along the gizzard and intestine. An adult taken in Greymouth on 8.ii.1973 also had massive deposits of abdominal fat. These observations are circumstantial evidence of preparation for migration in both adults and juveniles during late summer.

12. GENERAL ASPECTS

12.1 BREEDING-SEASON

Fig. 8.1 shows major events in the breeding of the shining cuckoo and its host. Except for the histograms of warbler-song (see section 8.1), the horizontal axes are marked in weeks beginning 7-13 July. Dates of "arrival" of the cuckoo are from Cunningham's national survey (1955a) of reports of first song in 1952 and 1953. The data are offset by two days: eg. Cunningham's week ending 22 July is plotted as 14-20 July for convenience. The histograms of laying, hatching and fledging of the cuckoo are combined data for three years at Kowhai Bush (see sections 10.2 and 11.1).

The monthly phenology of breeding in the two species is summarised as follows:

August (late winter) - warbler-song increases in intensity; warblers build first nests and begin laying; a few shining cuckoos arrive.

September (early spring) - warbler-song reaches maximum intensity coincident with a peak in laying; building becomes less frequent; warblers start hatching; cuckoos apparently arrive in greatest numbers.

October (mid-spring) - warblers sing intensively but rarely build; they seldom lay, but most early broods hatch and fledge; cuckoos lay first eggs.

November (late spring) - warbler-song intensifies and warblers re-build and re-lay; warblers continue to hatch and fledge; laying by cuckoos reaches a peak; some cuckoos hatch and fledge.

December (early summer) - warbler-song diminishes in intensity and building stops; laying (by warblers and cuckoos) tails off; late warbler-broods and most cuckoos hatch and fledge.

January (mid-summer) - warblers rarely sing and their last nestlings (warbler or cuckoo) fledge.

A major point is that when most shining cuckoos arrive in New Zealand (or at least start calling) warblers have already built their early nests and laid most early clutches. At Kowhai Bush cuckoos started laying seven weeks after warblers did. Similarly, in England the European cuckoo starts laying up to four weeks after several of its hosts have begun laying (though other hosts start laying even later than the cuckoo; Lack 1963).

Most laying by shining cuckoos was in the third quarter of November, about seven weeks after the peak of migration. The European cuckoo in England also shows a lag between migration and laying; most eggs are laid five weeks after the week during which most cuckoos arrive (Lack 1963). In southern Africa females of *Chrysococcyx caprius* start laying about a month after the first of them have arrived (Reed 1968). Lack suggested that in Europe the start of laying is related to the time the female cuckoo needs after migration to obtain enough nourishment to form eggs. A dietary interpretation of the lag is especially pertinent to shining cuckoos which supposedly fly 3 000 km to New Zealand without feeding en route. For shining cuckoos the lag is in October/November, a time when food is probably abundant and the maturation of gametes assured.

English cuckoos lay mainly during 10 weeks (Lack 1963), and the shining cuckoo's laying-season was also 10-12 weeks (section 10.2). *Chrysococcyx caprius* in southern Africa lays from late October to mid-January (11 weeks), though drought may curtail breeding (Payne 1973). The shining cuckoo's breeding-season (presence of eggs or nestlings; including data from the Nest Record Scheme) was 17 weeks (mid-October to early February). In southern Africa *Ch. caprius* breeds from late October to mid-March (19 weeks) and *Ch. klaas* breeds from late October to early January (10 weeks; Payne 1973). The seasonality and duration of the shining cuckoo's breeding is therefore very similar to that of its southern African congeners. Much presumably depends on climatic regime: in South-west Africa *Ch. klaas* lays from January to April (Jensen and Clinning 1974).

At Kowhai Bush shining cuckoos ceased laying in mid-December when summer was only beginning. However this is not surprising, since the host stopped laying at that time (section 8.1), and shining cuckoos probably need to accumulate fat before migration.

12.2 BREEDING-CYCLE

Incubation period exceeded nestling period in warblers, but the reverse was true of cuckoos. Yet the sum of these average intervals was similar in both species: 19.5 + 17.2 = 36.7 days for warblers, and 15.5 + 19 = 34.5 days for cuckoos. Thus, if a cuckoo lays at about the time the host starts incubating, the nestling cuckoo fledges when the host's own young would have fledged. At the other extreme, a cuckoo may lay a week after incubation begins (Fig. 10.2), in which case the foster-parents are tied to the nest for about a week longer than otherwise.

12.3 MORTALITY AND REPRODUCTIVE SUCCESS

Of eight cuckoo-eggs that failed to hatch, one was apparently infertile (containing no trace of an embryo despite a long period of incubation), two were broken on the ground beneath the nest (probably preyed upon), three disappeared without trace (possibly preyed upon), one I found abandoned, and another was laid in an apparently abandoned nest. Four cuckoos failed to fledge, of which three were preyed upon, judging by damage to the nest. The fourth nestling died at five days old on the day of a cold, wet southerly storm that ended a fortnight of warm weather. Without feathers (only sparse natal down) and having recently evicted its foster-siblings, the cuckoo possibly died of hypothermia.

and Fig. 8.2

Table 8.4 give the yearly and overall reproductive success of cuckoos against that of warblers. Figures for the two species are not directly comparable, because

a. the cuckoo's eggs and nestlings occurred singly, whereas a predator or gust of wind could destroy several warblers at once; and

b. one species was responsible for some mortality in the other.

There were major fluctuations between years in the success of cuckoos, but samples were small. The combined data suggest that whereas a cuckoo-egg had the same chance of hatching as a warbler-egg, nesting- (and therefore breeding-) success was higher for cuckoos. It may have been that defensive behaviour (against predators), exhibited by mature nestling cuckoos but absent in their warbler-counterparts, improved the chances of a cuckoo fledging.

The 70% hatching-success of shining cuckoos compares with 75% in *Chrysococcyx caprius* (southern Africa, n = 12; Hunter 1961) and 62% in *Cuculus canorus* (Europe; Niethammer 1938, cited by Payne 1974). The 75% nesting-success of shining cuckoos compares with only 43% for *C. canorus*. The 52% breeding-success in New Zealand compares with 58% for *Ch. caprius* and about 25% for *C. canorus* (Payne 1977). Thus success appears to be lower in Europe than in the Southern Hemisphere.

12.4 SIZE OF HOME RANGE

To my knowledge, the colour-marking of cuckoos in an area has never been attempted with success, and facts on social organisation are lacking. Some authors (eg. Payne 1967, 1977; Jensen and Vernon 1970) speculated that brief pair-bonds, no pair-bonds, polygamy, polygyny or promiscuity occur in cuckoos (including *Chrysococcyx*), and others (eg. Friedmann 1968, Lack 1968: 84) considered monogamy more likely.

The laying-ranges of *Cuculus canorus* may overlap by several hundred metres (Blaise 1965, cited by Payne 1973). However, Wyllie (1975) quoted and accepted Chance's contention that females of *C. canorus* maintain a territory from which they deter others. Jensen and Vernon (1970) reported strong territorialism in *Chrysococcyx caprius* and the possibility of defended "laying territories". In south-western Australia pairs of *Ch. lucidus plagosus* establish "definite territories, usually of considerable area" (Ford 1963).

On six separate occasions (from 3 to 22.xi.1978) I saw in a restricted area of Kowhai Bush, a banded shining cuckoo (see section 9.3). The sightings of this bird (Fig. 12.1) show that it occupied at least five warbler-territories with a combined area that year of 4.4 ha, or, more likely (including intervening areas), that it covered about nine warbler-territories or 8.3 ha (average territory in Habitat 1 = 0.92 ha; Table 3.1). On at least five of the occasions the cuckoo had a single companion, and I saw no other cuckoos in the area during November. Since November is the modal month of laying at Kowhai Bush (Fig. 10.1), the observations suggest that at least during laying shining cuckoos may occupy exclusive home ranges and be monogamous.

In a census of breeding birds on Taranga Island (Hen and Chickens group), Turbott (1940) reported three pairs of shining cuckoos in 75 acres of forest (= 10.1 ha/pair). Kikkawa (1966) estimated that there was one pair of cuckoos per 21.9 ha of *Nothofagus*-forest (inland Nelson), and one pair per 4.9 ha of modified forest (south-eastern South Island). In South-west Africa, a male *Chrysococcyx klaas* called over an area of at least 30 ha, and morphologically similar eggs attributed to one female were found within 16 ha (Jensen and Clinning 1974). Thus the area shown in Fig. 12.1 is of the correct order of magnitude for a glossy cuckoo's home range.

I suggest that in theory the area occupied by a cuckoo can be related to the number of eggs a female lays in one season. The latter is difficult to determine, but Payne (1973) estimated it for three African glossy cuckoos. Histological examination of ovaries showed the number of eggs ovulated in two weeks, and seasonal production was determined from the length of the laying-season. The average weekly rate of laying was 1.3-1.8 eggs in 25 *Ch. caprius*. If these values hold generally for the genus then female shining cuckoos, which lay during 10 weeks at Kowhai Bush (section 10.2), could each produce 13-18 eggs in a season.

For cuckoos that parasitise only one host, the number of eggs that a female lays in a season (n), multiplied by the average area of a host's territory (H), and divided by the frequency of parasitism (p), gives the minimum area that supports the female in her reproductive activities (C), i.e. $C = H\ n/p$. Females may hold exclusive home ranges

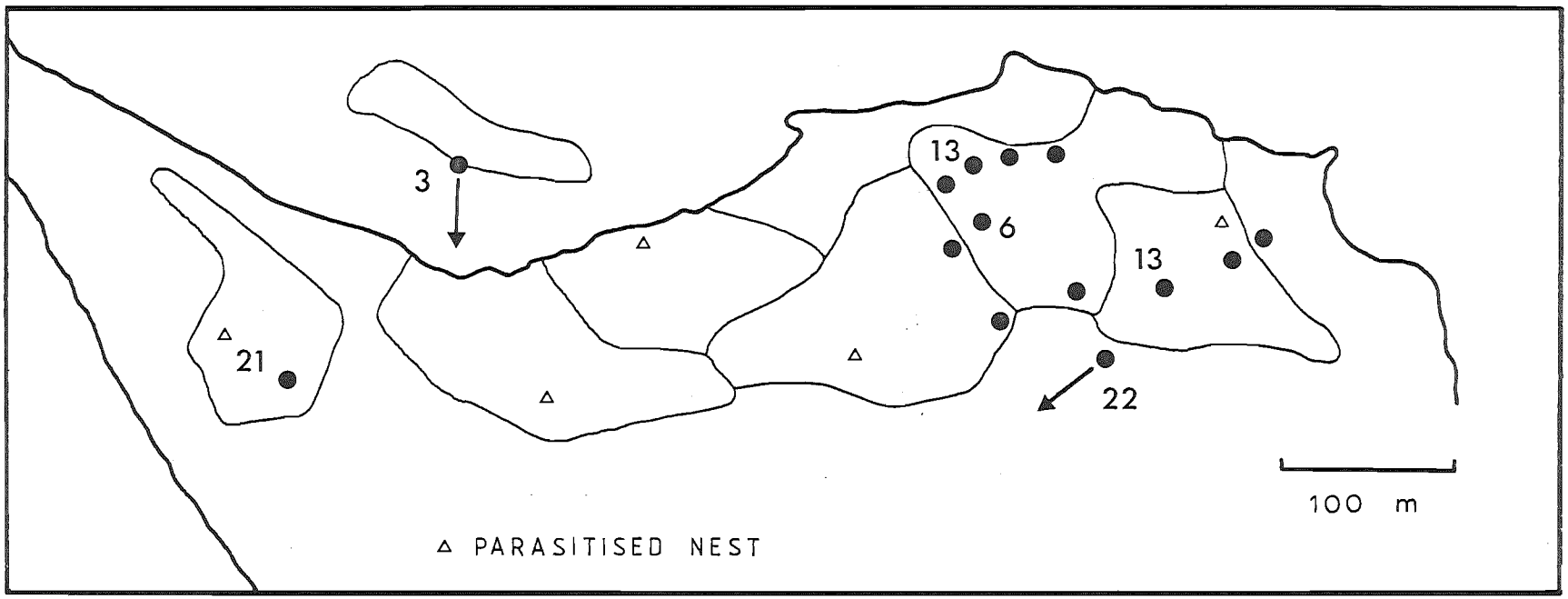

Figure 12.1 - Sightings of shining cuckoo B-40201 at Kowhai Bush. Thin lines show concurrent warbler-territories (see Fig. 3.1d); numbers are dates in November 1978; arrows show the cuckoo's direction of flight. All five late nests that I found in the area were parasitised.

of size C, or if ranges overlap, each female must search an area larger than C. If a female cuckoo finds and parasitises every nest (p = 1), then C = H n. As the frequency of parasitism falls to nil, cuckoos must search increasingly large areas.

Assuming that a shining cuckoo at Kowhai Bush lays 16 eggs in a season, then, since the frequency of parasitism at Kowhai Bush is 0.55 (section 10.4), one cuckoo associates with 16/0.55 = 29 warbler-nests. A pair of warblers occupies 0.68 ha on average (Table 3.1), so a female shining cuckoo at Kowhai Bush may require exclusive use of 20 ha, or search an area of at least that size. In practice the area may be smaller, since a cuckoo could lay twice in one warbler-territory if the warblers lost a clutch and nested twice. The 20 ha predicted exceeds that observed (8 ha), but the latter is a minimum since observations were piecemeal.

If female cuckoos require 20 ha each at Kowhai Bush, then in the entire 240 ha of forest, perhaps only 12 females breed. In my main study-area of 30 ha only one or two females may have been active. My daily observations in three summers suggested that cuckoos were few and far between, and I saw or heard them only 14 times during 123 5-minute stationary bird-counts between October and January 1976/77 (bird-count stations shown in Fig. 2.2).

12.5 EFFECT ON HOST

There are three ways in which the shining cuckoo reduces, or might reduce, the reproductive success of its host. First is the possibility, as yet unobserved, that shining cuckoos steal eggs (and even young) from warbler-nests (see section 8.2). This might cause desertion of a nest too advanced for parasitism, and induce re-nesting to the cuckoo's advantage (Payne 1977). Second, it is inferred (section 10.1) that a female cuckoo removes a warbler-egg when laying her own. If the cuckoo's egg is infertile, or if the cuckoo-nestling dies at an early age, then the warbler's brood is partially reduced.

However, the major influence of the cuckoo is exerted by the nestling, which, if it survives to evicting-age, completely destroys what remains of the warbler's clutch or brood. This overrides the previous effect. A fourth factor, listed by Payne (1977), that the long nestling period and juvenile-dependency of cuckoos may delay re-nesting by the host, scarcely applies here since there is usually no time for warblers to re-nest after rearing a cuckoo (or second successful brood of warblers).

Of 70 warbler-eggs in 20 unparasitised late nests, 23 eggs (32.9%) survived to produce nestlings which fledged. Of 53 warbler-eggs in 16 parasitised nests, only one warbler-egg (1.9%) produced a fledgling (the cuckoo-egg was infertile). Therefore parasitism caused the loss of 31 warbler-fledglings for every hundred late warbler-eggs laid. This value (31%) multiplied by the frequency of parasitism (55%; section 10.4) gives 17.1%, the calculated amount by which production of the host's late progeny is reduced (Payne 1977). Thus, of every 100 late warbler-eggs, only 17 failed because of parasitism to produce nestlings that survived to fledging. This figure is even lower than many given by Payne (1977; table 1) for cowbirds (*Molothrus*) and *Clamator jacobinus* where the host's young are raised with the parasite. Parasitism has little effect on the fledging-success of grey warblers because mortality from other causes is so high, and because the frequency of parasitism is relatively low.

Cuckoos in general apparently have little adverse effect on the survival of hosts over broad areas (Payne 1977), and Lack (1963) concluded that *Cuculus canorus* "is an almost negligible cause of egg and nestling losses among English breeding birds".

12.6 GROWTH AND FEEDING OF BROODS

An idea implicit in some popular writings is that the nestling shining cuckoo is an excessive imposition on the resources of the foster-parents. For example, Oliver (1955: 477) referred to the cuckoo as a "villain (that) is fed by the hard working warbler". There may be some truth in the assertion Chalton (1976) found that a pair of *Ploceus ocularis* in southern Africa lost on average 8.8% of their weight while feeding a nestling *Chrysococcyx caprius*, but there are no figures for the weavers feeding their natural young. I tested the null hypothesis that a nestling cuckoo required of its foster-parents the same effort in feeding as a brood of their own young, by comparing the growth and feeding of single shining cuckoos, with that of broods of 2-4 warblers.

Fig. 12.2 shows changes in the total weight of unparasitised broods of 2-4 warblers against the growth in weight of nestling cuckoos (Table 11.2). I added individual weights of warblers in a brood and included the sum only if the brood was complete. For example, if one nestling in the brood died I disregarded subsequent data. The data is for early and late broods combined. For cuckoos day 0 was that of hatching; data for warblers start with day 1, on which the first nestling in the brood hatched.

Obviously, at all times, the fewer the warblers the lesser was their

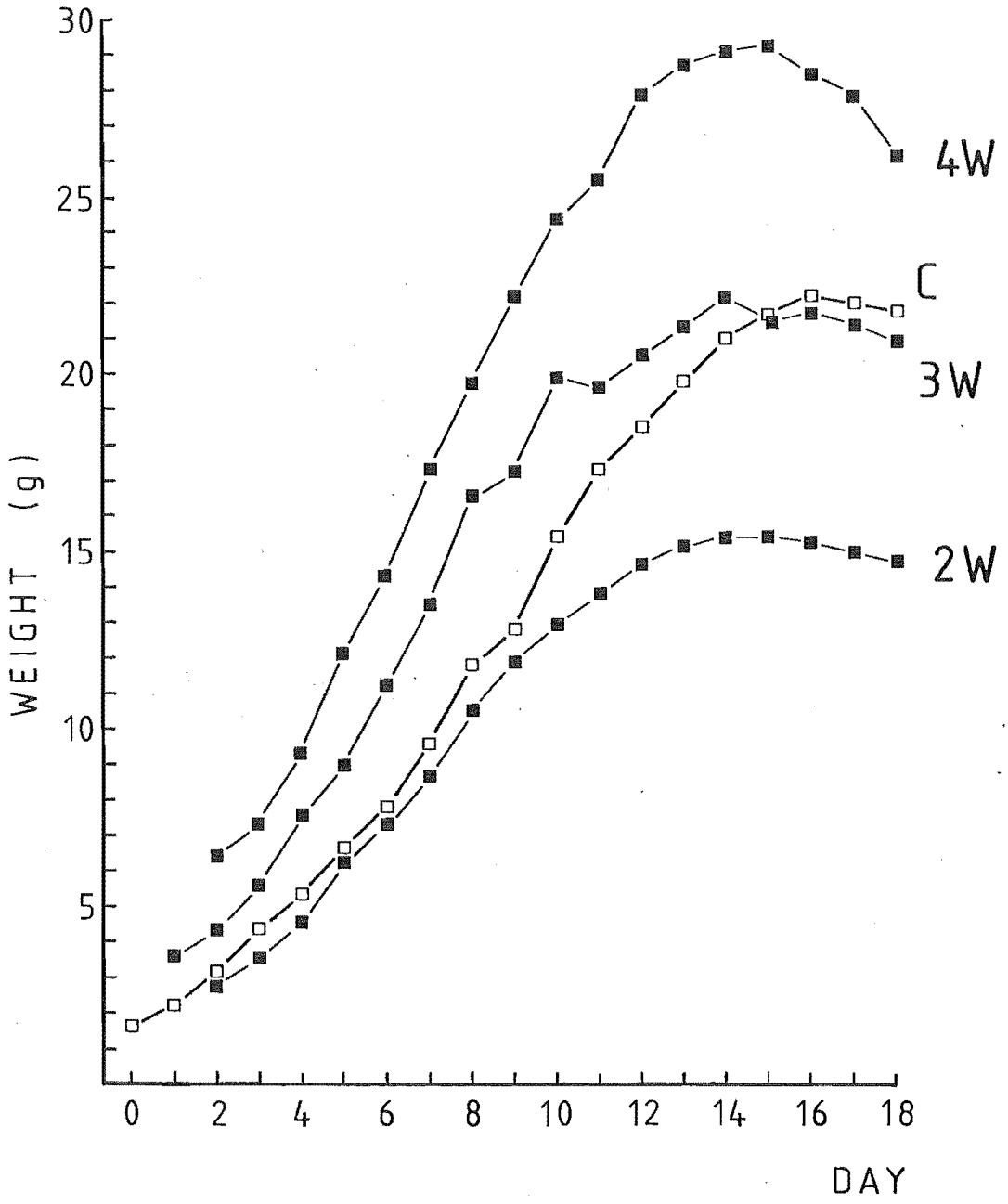

Figure 12.2 - Mean weights of single nestling cuckoos (C) and whole broods of 2-4 warblers (W) as a function of age (cuckoos) and days since the first nestling of the brood hatched (beginning day 1; warblers). Sample-sizes: cuckoos 3-7, four-warblers 2-12, three-warblers 2-8, two-warblers 3-7.

combined weight. Warbler-broods show recessions in total weight during the last 3-4 days before fledging, just as do the curves for individual warblers (section 6.5). In terms of weight one cuckoo was about equivalent to two warblers for the first nine days, and then it grew to reach a final weight approximately that of three warblers. Single cuckoos never weighed as much as the four warblers that were often raised. This implies that a cuckoo only moderately taxed the foster-parents' ability to provide food, unless cuckoos had a higher metabolic rate than warblers. The latter is unlikely because cuckoos received fewer visits/hour throughout their nestling period than three or four warblers (see later). Also, a single cuckoo is probably energetically more efficient than several warblers of the same weight, because it more closely approaches a sphere.

In 1977/78 and for the second half of the breeding-season in 1978/79, I recorded the frequency with which warblers fed broods that comprised one cuckoo or three or four warblers. (There was no time to devote to broods of two, which were scarce anyway.) I combined all data (both years and early/late broods) since samples were relatively small: 36 hours' observation of warblers in broods of four, 17 hours on broods of three, and 41 hours on cuckoos (total = 94 hours or 1230 visits by a warbler). I included in the analysis only nests with the full complement of nestlings, and disregarded those containing unhatched eggs, or a cuckoo with warblers yet to be evicted. The basis of comparison between broods was the "day of feeding", day 1 being that on which the first nestling hatched.

In passerines, the rate at which parents bring food to the nest may vary with season (ie. between early and late broods), with individual pairs, and with brood-size (the variable of interest here). Royama (1966) warned that feeding-frequencies may not truly reflect consumption by nestlings, since the average weight of food delivered may not be constant - the number or size of items may vary. *Parus major*, which Royama studied, and the Snares Islands race of *Bowdleria punctata* (Best 1973), usually carry only one item of food to the nest at a time. Grey warblers, however, often took several, since I saw them continuing to forage, despite items already held in their bill. As for size, older nestling warblers were frequently fed items less than 5 mm long (section 6.7), and at the other extreme I sometimes saw them receiving (with difficulty) stick-insects (Phasmatida) 3-4 cm long. Despite these considerations I feel justified in pursuing the following analysis because my concern is not with quantifying consumption, but with comparing apparent effort required to feed one cuckoo as opposed to several warblers. "Effort" is as much a function of number of visits as of weight of food carried.

Fig. 12.3, the number of visits/nest/hour as a function of the day of feeding, shows:

A. That as nestlings matured (warbler or cuckoo) the adults visited the nest more frequently. This is to be expected since the nestlings' need for food will increase with their weight.

B. That broods of four and three warblers were visited with about the same frequency. Thus, on average, individuals in broods of four must have received fewer visits than those in broods of three (see later).

C. That a single cuckoo was visited less often than broods of three or four warblers. This implies that cuckoos required of their foster-parents less effort than an unparasitised brood, even allowing for the cuckoo's slightly longer nestling period.

Linear regressions (Table 12.1 a-c) of the number of visits/nest/hour on the day of feeding (raw, ungrouped data), suggest similar slopes for broods of three and four warblers, and a much lesser slope for cuckoos. The y-intercepts are much closer to the origin for cuckoos and warblers in broods of three, than for warblers in broods of four. Only the line for three-warbler-broods fits well. Comparisons of the regressions (broods of four vs. broods of three; broods of four vs. cuckoos) show the variances to be significantly heterogeneous (χ^2- test; $P < 0.01$).

Table 12.1 - Linear regressions of visits per nest per hour (a-c) and visits per nestling per hour (d,e) on day of feeding; W = warblers, C = cuckoos. All regressions significantly linear (F-test; $P < 0.01$).

	brood-size	n	r^2	regression-equation
a	4 W	39	0.43	y = 0.90x + 8.00
b	3 W	18	0.67	y = 1.24x + 3.36
c	1 C	41	0.31	y = 0.46x + 3.82
d	4 W	39	0.43	y = 0.22x + 2.03
e	3 W	18	0.67	y = 0.41x + 1.11

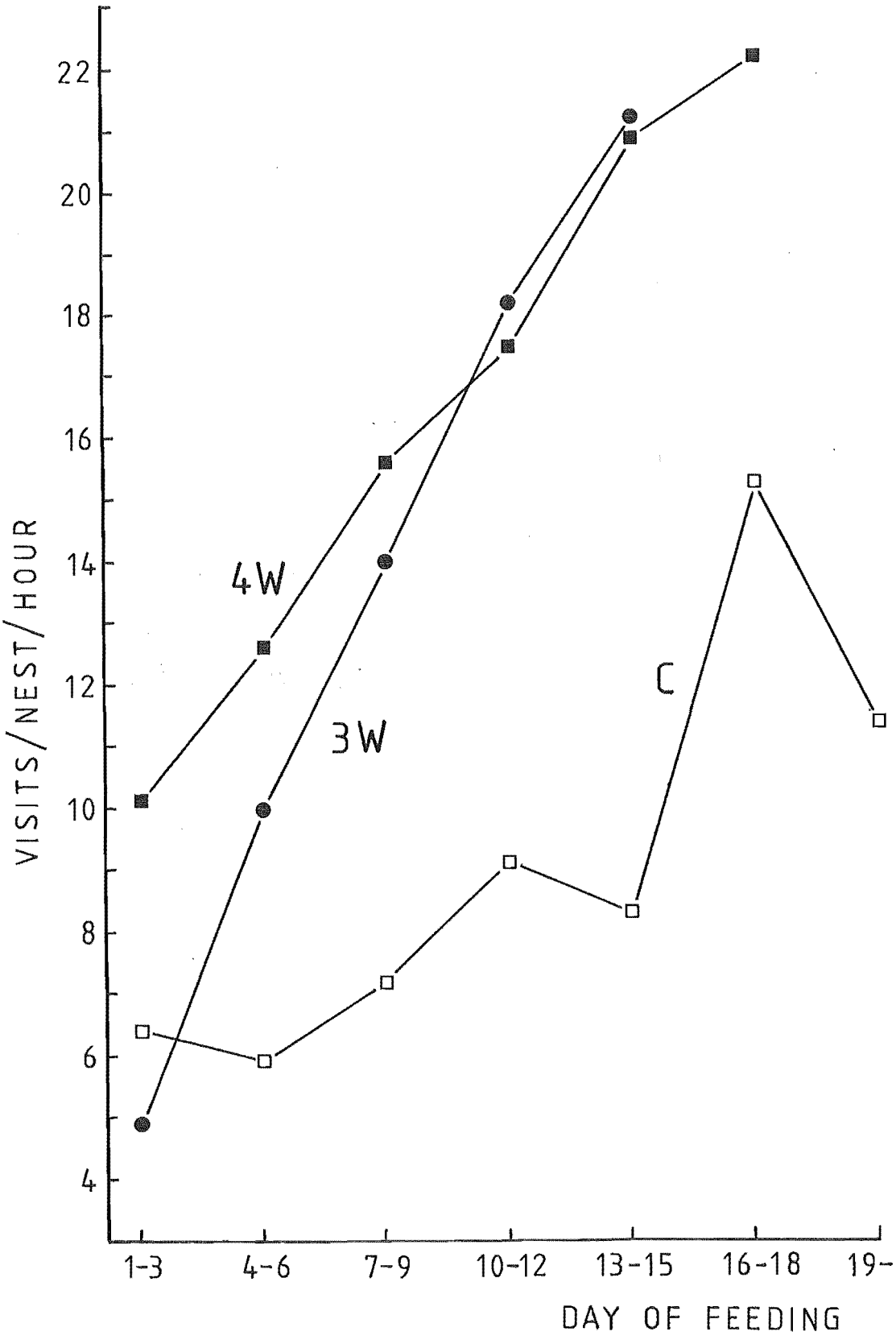

Figure 12.3 - Visits/nest/hour for cuckoos (C) and broods of 3 or 4 warblers (W) as a function of day of feeding. Each point based on 99-494 minutes' observation.

Fig. 12.4, the number of visits/nestling/hour as a function of the day of feeding, suggests that, except initially, individual warblers in broods of three were visited more on average than those in broods of four. Many studies of passerines (eg. Gibb 1950, Royama 1966) have shown that while the number of feeding-visits may be greater for larger broods (see warbler-curves in Fig. 12.3), the increase is not proportionate, so that on average members of large broods individually receive fewer feeds than those of smaller broods. Linear regressions of the raw, ungrouped data (Table 12.1d,e), suggest a steeper slope and smaller y-intercept for warblers in broods of three compared with those in broods of four. The variances are significantly heterogeneous ($\chi^2 = 60$; $P < 0.001$).

Fig. 12.5 gives the number of visits/nest/gramme-of-nest-contents/hour, as a function of the day of feeding. Parents maintained a constant number of visits/g to warblers in broods of three, but for cuckoos and warblers in broods of four visits/g declined as the nestlings aged. It could be that three warblers were the energetically optimal brood, or perhaps as cuckoos and warblers in broods of four developed plumage and homoiothermy, their food-requirement/g declined, while that of warblers in broods of three stayed uniform due to less efficient heat-conservation.

12.7 DISCUSSION OF PARASITIC STRATEGY

Female shining cuckoos perhaps expend energy, at least during laying, in asserting exclusive use of a home range (section 12.4). Otherwise they are free of the factors which normally attend breeding in altricial birds: cuckoos neither build, nor incubate, nor gather food for their progeny. However, since shining cuckoos specialise in parasitising one host that is territorial and breeds asynchronously (section 5.2), females may need to devote much time and energy to a protracted search for nests. This is implied by the inefficient parasitism of some nests (section 10.3) and by a frequency of parasitism less than unity (section 10.4). Circumstances may be such that it is advantageous if ovulation is timed for a particular nest and subsequent eggs are disposed of as occasion allows (Hamilton and Orians 1965).

Each female shining cuckoo perhaps lays 16 eggs in a season (section 12.4). At 1.85 g per egg (section 10.5) this is equal to 1.3 times the body-weight (29.6 g/23.1 g). A female warbler that breeds successfully would lay two clutches or eight eggs in a season, each egg weighing 1.5 g (section 5.5). This equals 1.9 times the body-weight (12 g/6.4 g).

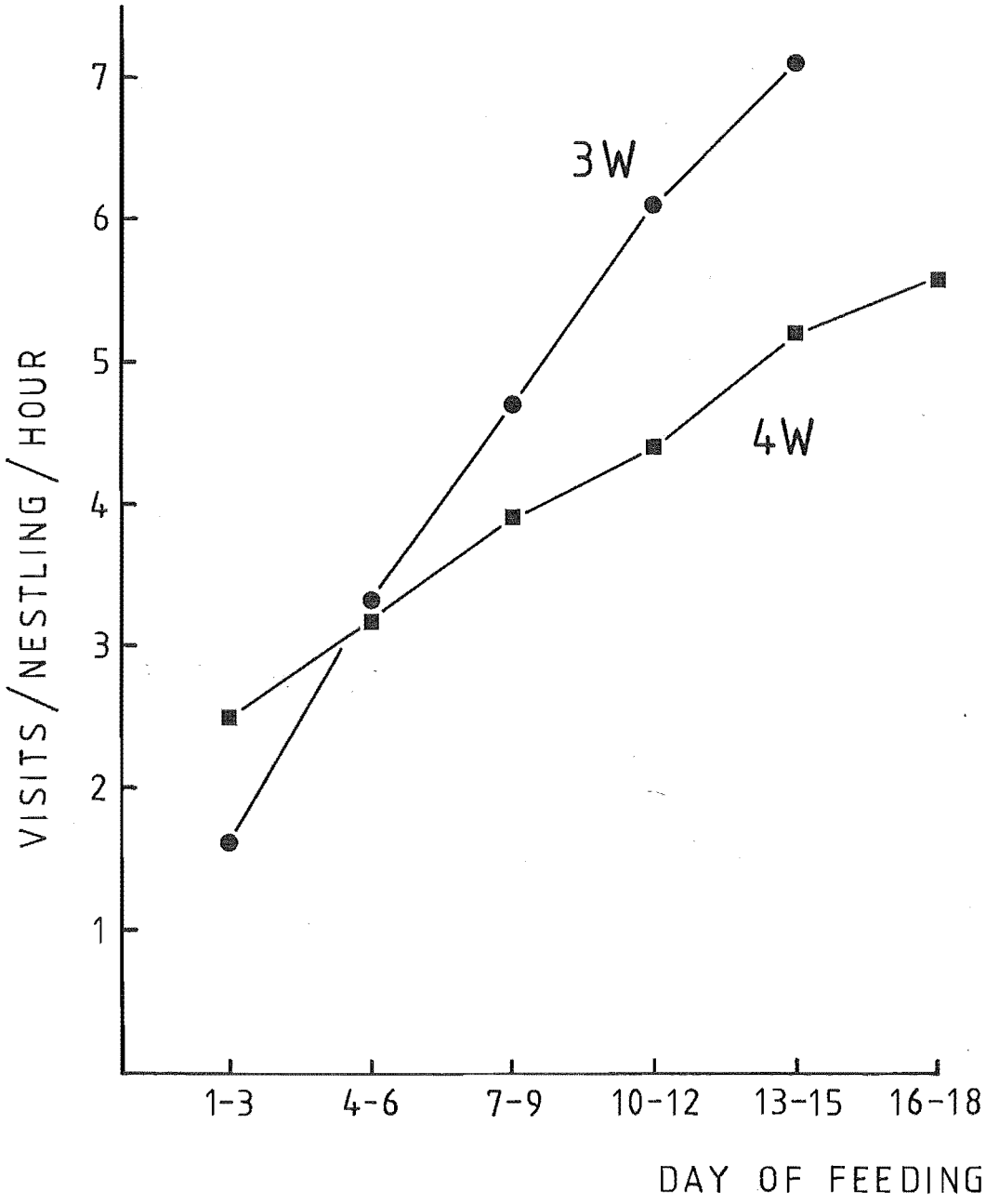

Figure 12.4 - Visits/nestling/hour for broods of 3 or 4 warblers (W) as a function of day of feeding. Sample-sizes as in Fig. 12.3.

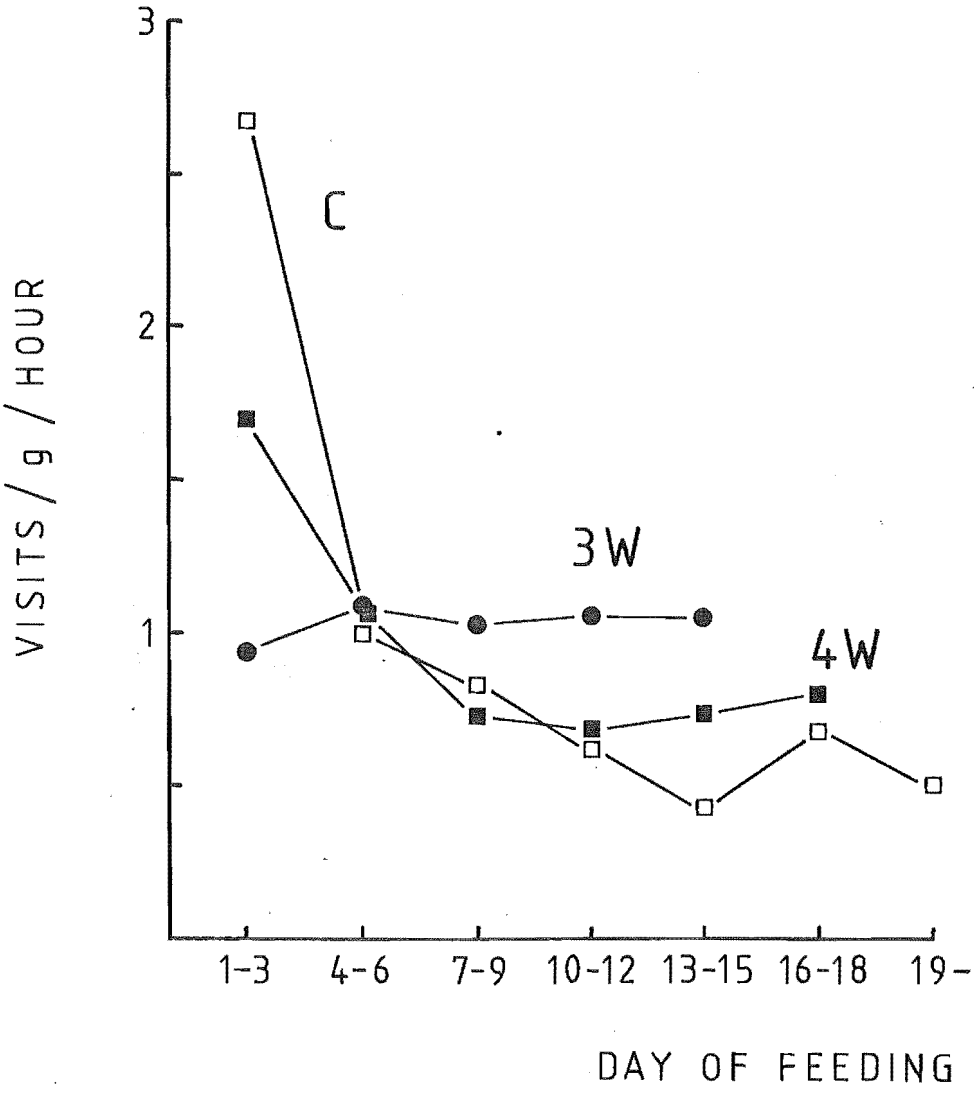

Figure 12.5 - Visits/hour divided by total weight of nest-contents for cuckoos (C) and broods of 3 or 4 warblers (W) as a function of day of feeding. Sample-sizes: cuckoos 2-8, four-warblers 3-9, three-warblers 2-5.

The laying by shining cuckoos of many small eggs distributed among as many nests, and the laying by warblers of fewer eggs that are larger in relation to body-weight, are probably energetically equivalent. The cuckoo's strategy, of course, has advantages in terms of matching the host's size of egg, and (presumably) in enhancing reproductive success.

The cuckoo's parasitic efficiency and the warbler's ability to maintain its numbers are presumably in balance. Essential to this balance may be factors imposed on the cuckoo by physical difficulties such as the parasitism of only late clutches, and a less than maximum frequency of parasitism.

A recent stress on the host-parasite equation may be the effect of predation by exotic mammals. Predators directly reduce the reproductive success of cuckoos by destroying their eggs and young (section 12.3), but there may also be competition. Of warbler-eggs laid in the late half of the season, some may need to survive if warblers are to maintain their numbers, some will be destroyed by cuckoos and predators, and any surviving the other causes of mortality may contribute to a non-breeding reserve of individuals.

In three summers I observed 119 warbler-eggs or -nestlings in late nests (mostly in the main study-area). Of these, 24 (20.2%) survived to fledge, cuckoos destroyed 34 (28.6%), 43 (36.1%) certainly or possibly fell prey to mammals, and 18 (15.1%) died from other causes. Since less than five fledglings were apparently recruited to the breeding-population of the main study-area per year (section 7.4), brood-parasitism and predation seem not to threaten the survival of warblers (bear in mind the production of early fledglings, and the high post-fledging survival - section 7.2). The interesting reflection is on the losses to predators, and whether they represent eggs and nestlings denied to the cuckoo.

Selective pressure to refine the shining cuckoo's parasitic strategy seems to have been weaker than for many other brood-parasites. The reduction in egg-size relative to adult weight is small (section 10.5), partly because the host's eggs are large relative to its body-weight. The host displays no anti-parasite adaptations, and the cuckoo's egg is non-mimetic (section 10.5). A long incubation period (relative to that in other glossy cuckoos; section 10.6), the lateness of eviction (section 11.2), and the tendency to lay late in the warbler's incubational cycle (section 10.3), often lead to interspecific competition for food among nestlings. Yet parasitism often succeeds despite this.

One wonders to what extent the warbler's breeding-strategy (which I relate to properties of the food-supply; section 8.3) has influenced the shining cuckoo's breeding-cycle. For example, the warbler's incubation period is longer than expected, perhaps partly because the female incubates alone and is not fed by the male. The shining cuckoo's long incubation period could be due to the foster-mother's incubational routine, or it may be merely that selection for a short incubation period is weak when the host incubates for so long. New Zealand's original lack of predators may have permitted poorly-timed parasitism that lengthens the life of the nest.

Do warblers breed early as an adaptation to ensure that their first clutches escape parasitism? I think not, because other insectivorous birds in New Zealand breed at least as early as grey warblers (Appendix 1) but lack brood-parasites. Thus, an ecological interpretation of early breeding, relevant to all species (section 8.3), is more likely. Provided there is sufficient food to nourish the young, natural selection, through its philoprogenitive tendencies, will probably favour early breeding and double-broodedness anyway.

Do individual warblers lay larger clutches early in the season than later to minimise losses from brood-parasitism? Apparently not, since there was no significant difference between the size of early and late clutches (section 5.6). Unparasitised late broods were smaller than early broods (Table 6.4), but this must reflect differential mortality from factors other than brood-parasitism. Whether some pairs of warblers ceased breeding after their initial attempts, so avoiding parasitism, I did not fully resolve (section 8.1).

If rearing a cuckoo physically taxed warblers more than did a brood of their own young, parasitism might less often succeed. However, the life of the nest is not extended (provided the cuckoo lays at about the time incubation begins; section 12.2), and fledgling cuckoos are probably dependent for no longer than warblers (section 11.6). Although a cuckoo is brooded in longer spells and for more of the nestling period than is a brood of warblers (section 11.5), it is visited with food less often (section 12.6). Thus, the relative ease with which a cuckoo is seemingly reared may have helped to promote parasitism.

CONCLUSION

This study answered questions on how grey warblers and shining cuckoos breed. Warblers raise several small families slowly during a long breeding-season. The breeding-cycle is protracted, the eggs and nestlings are heavy relative to adult weight, the laying-interval is unusually long, adults are relatively long-lived, and few juveniles join the adult population each year. This strategy, which is similar to that of some other New Zealand and temperate Australian passerines, may be a response to a relative shortage of food during breeding. Shining cuckoos, which parasitise late warbler-nests, lay eggs that are non-mimetic but similar to the host's in size. Cuckoos often lay after the host starts incubating and a short period of interspecific competition between nestlings is common. The young cuckoo eventually evicts all other nest-contents and is reared alone. Brood-parasitism has little effect on the reproductive success of warblers, and a nestling cuckoo is less arduous to feed than a brood of three or four warblers.

SUMMARY

I studied breeding in grey warblers (Gerygone igata) and shining cuckoos (Chrysococcyx lucidus lucidus) at Kowhai Bush, near Kaikoura (South Island, New Zealand), during three summers (1976/77-1978/79). I colour-banded 188 warblers and 11 cuckoos, examined 98 occupied nests and recorded the dates of laying of 22 cuckoo-eggs and over 240 warbler-eggs.

1. GREY WARBLERS

TERRITORIES. Warblers held exclusive self-contained territories while breeding, and occupied larger overlapping home ranges during winter. Breeding adults were sedentary all year. Territories were 0.68 ha on average. Those in tall,dense forest ($\bar{x}$ = 0.45 ha) were significantly smaller than those in stunted, open forest ($\bar{x}$ = 0.92 ha), possibly reflecting different concentrations of food. The average annual mortality of breeding warblers was 18.5%, and the average life-expectancy 4.9 years. At the end of the study the oldest marked warbler had lived at least 44 months.

NESTS. The enclosed nest was built by the female, who was never fed by the male. Building of early nests took 2-4 weeks, and was followed by a delay of 2-8 days before laying. Entrances were non-randomly orientated but apparently not in direct relation to prevailing winds. Nests were 3.5 m above ground on average. Late nests were lower than early ones and sited in shorter trees. Warblers usually built in the upper half of the tree nested in, but in the lower half of the distance from ground to canopy. On average they built closer to the canopy in stunted forest with no understorey than in denser forest.

EGGS. Warblers laid during 15-16 weeks in two main bouts. First clutches were initiated asynchronously during 5-6 weeks. Eggs of a clutch were laid 48 hours apart, a phenomenon unknown in song-birds of the Northern Hemisphere, but shared with some other Australasian species. Fresh warbler-eggs were 1.49 g on average, or 23% of the mean adult weight (6.4 g). The average clutch-size was 3.93, the mode four, and the range 3-5. Incubation began with the completion of the clutch. Only females incubated, and it occupied about 70% of their time. The incubation

period was 17-21 days ($\bar{x}$ = 19.5 days).

NESTLINGS. Warblers hatched from the large egg relatively heavy - at about 1 g or 16% of the maximum average nestling weight. Broods of nestlings hatched during 0.3-2.1 days. On average 2.9 nestlings hatched per unparasitised nest and 1.7 nestlings fledged. Nestlings apparently changed weight according to a truncated normal curve, whereby the maximum weight preceded a recession. (Most passerines have sigmoidal patterns of growth.) Nestlings exceeded adult weight during development by up to 40%, which is unusual. The recession was apparently due to loss of water. Nestlings 10 days and older were fed entirely on invertebrates (mainly caterpillars), and more than 40% of items were 1-5 mm long. Nestlings in broods of two reached higher maximum and final weights than those in larger broods. Warblers in broods of four individually received fewer feeding-visits on average than those in broods of three. The nestling period was 15-19 days ($\bar{x}$ = 17.2 days).

JUVENILES. Parents fed fledglings for up to 35 days. At least 81% of fledglings survived 18 days. Most juveniles apparently dispersed from their natal area at independence, and the annual rate of recruitment to the breeding-population was about 5%. Meagre data suggest that some warblers bred the summer after that in which they were raised, while others experienced deferred maturity, perhaps in response to socio-environmental conditions.

BREEDING-SEASON. Warblers spent six months breeding. They built from late July to late November, and laid from late August to late December. Nestlings hatched from mid-September to early January, and fledged from early October to late January. Breeding was 1-2 weeks earlier in 1977 than in 1976. Warblers ceased laying in early summer, perhaps because of the late summer drought. Apparently there was a single moult which was post-nuptial. The interval between fledging of a brood and initiation of another clutch was 14-42 days. The breeding-cycle from laying to fledging was 43.7 days on average. Apparently there was no time for a pair to raise more than two successful broods per season.

REPRODUCTIVE SUCCESS. Of nests receiving eggs, 42% yielded at least one fledgling warbler. Of eggs failing to hatch, 32% disappeared without trace (many probably taken by mammals), and

cuckoos destroyed 22%. The greatest single cause of mortality of nestlings was mammalian predation. Of 265 warbler-eggs, 70% hatched and 38% yielded a fledgling. Of 185 nestlings 54% fledged. Late nests were less successful than early ones, probably because of brood-parasitism and an apparent increase in mammalian predation later in the season. On average each pair of warblers made 2.7 nesting-attempts per season, each female raising 2.0 fledglings.

BREEDING-STRATEGY. The grey warbler's breeding-strategy is similar to that of some other temperate Australasian song-birds, and may be an adaptive response to a relative scarcity of food during the breeding-season. Former freedom from predation may have facilitated the evolution of this strategy.

2. SHINING CUCKOOS

HOSTS AND MIGRATION. The grey warbler is almost certainly the shining cuckoo's sole host on the New Zealand mainland. A cuckoo which fledged from Kowhai Bush in December 1976 was present (and possibly bred - I saw it in 8 ha of forest embracing about nine warbler-territories) a kilometre from its natal area in November 1978.

EGGS. Parasitised nests received single cuckoo-eggs that were apparently swapped for a host's egg. Shining cuckoos lack egg-mimicry, perhaps because the warbler cannot see eggs clearly in the enclosed nest. The cuckoo's egg was only fractionally heavier and larger than the warbler's, and when fresh weighed 1.85 g or 8% of adult weight (23.1 g). Few species of cuckoo have eggs as large relative to adult weight. Shining cuckoos laid during 10 weeks, from mid-October to mid-December. The modal week of laying was the third quarter of November, seven weeks after the apparent peak of migration. Cuckoos started laying seven weeks after warblers did, and the host's first clutches escaped parasitism. Relative to the host's cycle, cuckoos laid from the day of the warbler's penultimate egg, to seven (or more) days after completion of the warbler's clutch. The laying of some eggs so late was inefficient, because it led to competition for food with nestling warblers. The average frequency of parasitism at Kowhai Bush was 55% of late nests. Cuckoo-eggs hatched in 13-17 days, depending on the time of laying relative to the host's cycle. Of 23 cuckoo-eggs, 70% hatched and 52% yielded fledglings.

NESTLINGS. Cuckoos hatched during November and December, and fledged from late November to late January. The nestling period was 19 days. At 3-7 days old cuckoos evicted from the nest all eggs or other nestlings. Cuckoos usually hatched before any warblers, but the delayed eviction often allowed some warblers to hatch and compete briefly for food. As possible aids to eviction, shining cuckoos grip the nest soon after hatching, tend to hold the wings out stiffly until 7-8 days old, and have a large flat back with bilateral spinal pterylae. Mimicry of the nestling warbler by the newly-hatched cuckoo is suggested by the latter's grey skin, white natal down and white rictal flanges. Natal down has not been reported in other parasitic cuckoos. The growth in weight of nestling cuckoos was sigmoidal, with the weight at fledging close to that of adults. The maximum average daily increase in weight was 2.6 g. Of 16 nestlings, 75% fledged. I saw foster-parents feeding fledgling cuckoos for up to 28 days.

3. INTERACTIONS

Parasitism had little effect on the reproductive success of warblers. The calculated reduction by parasitism of the production of late fledgling warblers was only 17%. Nestling warblers were brooded for up to 10 days; cuckoos for up to 16. On average brooding-spells were significantly longer for cuckoos than for broods of warblers. Thus brooding by warblers was exogenously modified. For the first nine days a nestling cuckoo was equivalent in weight to a brood of two warblers, then it increased to approximately the weight of three. A brood of four warblers far exceeded a single cuckoo in weight. A nestling cuckoo was visited less often on average than broods of three or four warblers, suggesting that cuckoos involved the foster-parents in less effort than an unparasitised brood.

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Lastly I must confess and record how very lucky I was for the opportunity to work in excellent circumstances, on a bird (the warbler) that is easily New Zealand's most charming.

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APPENDIX 1 - Details of breeding in the small arboreal native passerines studied to da... Acanthisitta is in the sub-order Tyranni; the others are song-birds (sub-order Passeres). * = Sub-families of the Muscicapidae. Type of nest: C = cupular, E = enclosed, H = in a hole, Cr = in a crevice. A blank indicates no information; B = both sexes.

species	adult weight (g)	nest	building	time to build (days)	delay before laying (days)	laying interval (hours)	clutch-size ($\bar{x}$, range)	incubation/brooding	incubation period ($\bar{x}$, range; days)	nestling period ($\bar{x}$, range; days)	juvenile dependency (days)	duration of breeding-cycle (1st egg to fledging; days)	broods per season	♂ feeds ♀	breeding-season	authority
Acanthisitta chloris (Xenicidae)	6-7	H	B	7-28	2-14	48	4.5 3-5	B	* 19-21	21-27		c.51	1-2	no	Aug - Jan	Gray (1969); Gaze (1978); Fitzgerald & Gaze (in preparation)
Bowdleria punctata (Sylviinae*)	34	C	B	3-14		24	2.4 2-3	B	16.1 15-18	20-21	35-40	39				Best (1973)
Gerygone igata (Acanthizinae*)	7	E	♀	7-27	0-8	48	3.9 3-5	♀	19.5 17-21	17.2 15-19	28-38	44	2	no	Aug - Jan	this study
Rhipidura fuliginosa (Muscicapinae*)	8	C	B			24	3.4 3-5	B	14.1 13-15	12.4 12-14		30	2-3	yes	Aug - Feb	M. Powlesland, pers. com
Petroica macrocephala (Muscicapinae*)	11	C or Cr	♀	4-5	8-10	24	3-5	♀	16-20	17-22	18-28		2-3	yes	Sep - Feb	Best (1975); P. Rearton, pers. comm.
Petroica australis (Muscicapinae*)	35	C	♀	2-7	2-7	24	2.8 2-4	♀	18	20.8 20-24	30-48	42	2-3	yes	Jul - Feb	Flack (1973, in preparation); R. Powlesland, pers. comm.
Zosterops lateralis (Zosteropidae)	13	C		6-13		24		B	11-12	9-11	16-21		3		Sep - Jan	Fleming (1943)

APPENDIX 2 - Architecture of the nest.

I measured the dimensions of nests (Fig. A1) to the nearest 0.5 cm, only one parameter (inside depth below entrance) requiring the nest's destruction. The results (Table A1) indicate that entrances were commonly round (3 x 3 cm), the smallest being 2.0 x 2.0 cm. The deepest entrance (6.0 cm) was also one of the widest (3.5 cm). The outside depth of an exceptionally low-slung nest was 21.0 cm. On average nests were slightly wider laterally than frontally. Lengths of beard (or tail) and of hood (or portico) varied extensively and were usually taken arbitrarily, because the base of the hood often merged imperceptibly with the body, and the beard sometimes extended as a single twig or straw to misleading lengths.

Table A1 - Measurements of nests (cm); see Fig. A1 .

	$\bar{x}$	n	s	range
A. width of entrance	2.9	61	0.33	2.0-3.5
B. depth of entrance	2.8	61	0.68	2.0-6.0
C. outside depth	14.0	58	1.65	10.0-16.5 (21.0)
D. inside depth below entrance	4.0	27	1.08	2.0-6.0
E. outside frontal diameter	7.2	56	0.72	5.5-8.5
F. outside lateral diameter	7.5	55	0.81	6.0-9.0
G. length of beard	6.6	35	3.85	2.0-19.0
H. length of hood	2.9	49	0.87	1.5-4.5

Nearly every nest (94%, n = 92) was attached to living vegetation, and the exceptions, although attached to dead twigs, were often surrounded by live foliage from adjacent branches. Every nest (n = 88) had an upper attachment beneath which it was slung, and 46% were truly pensile in having no, or negligible, other connections. However, 41% of nests had significant lateral points of attachment, and 28% were secured below. Considered another way, of the 88 nests, 25% had lateral attachments but none below, 13% were attached below but not laterally, and 16% had both attachments. In general, nests were of two types - those hanging more or less freely, and those secured in a matrix of surrounding twigs.

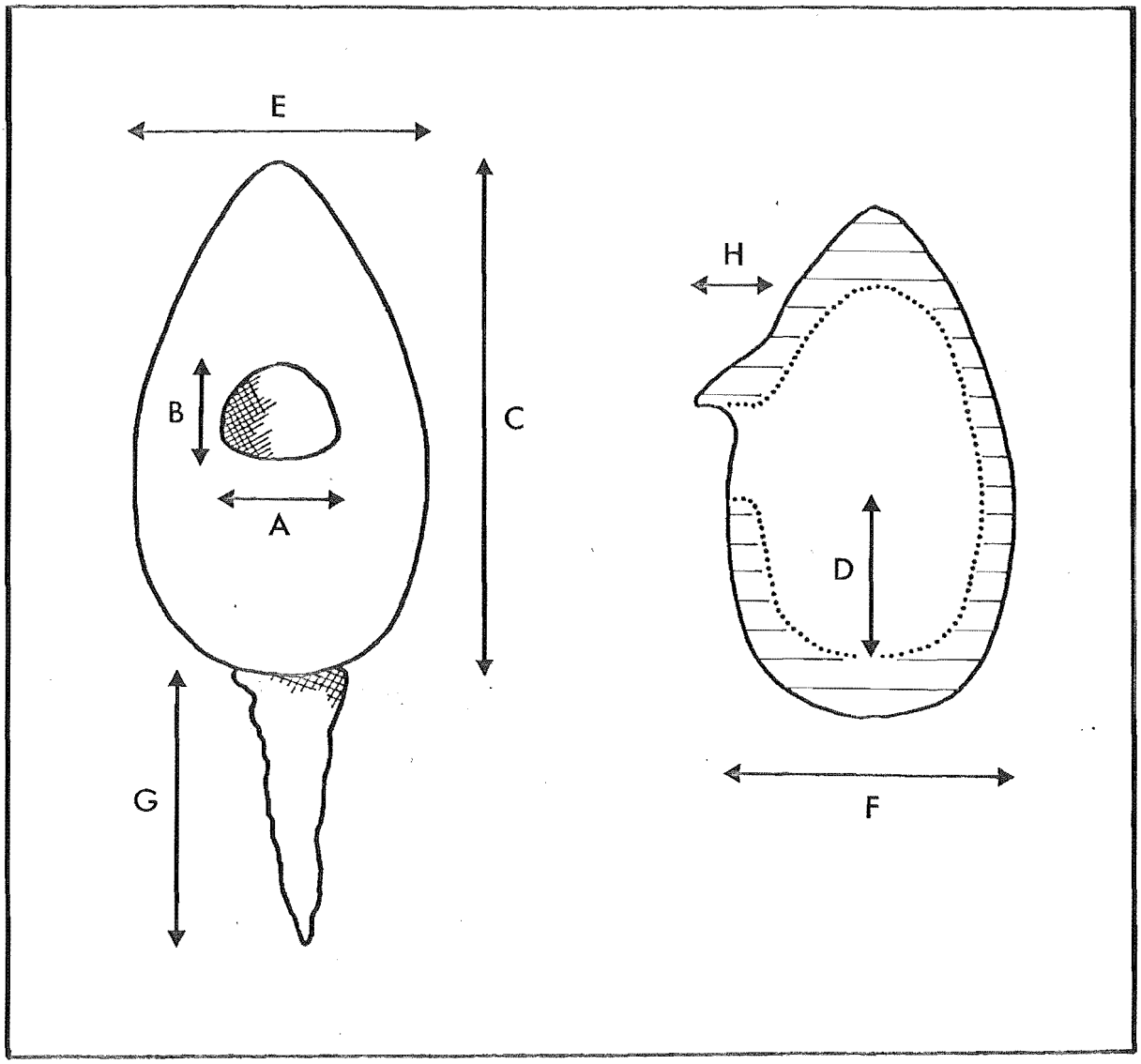


Figure A1 - Dimensions of nests: (A) width of entrance, (B) depth of entrance, (C) outside depth, (D) inside depth below entrance, (E) outside frontal diameter, (F) outside lateral diameter, (G) length of beard, (H) length of hood.

Beards were present on 63% of nests (n = 89), and they either hung freely, perhaps enhancing crypticity, or were involved in attachment. A hood above the entrance was a feature of 94% of nests (n = 88), of obvious value against the elements, and in 14% (n = 81) something of a threshold (Andersen 1926: 49) or ledge extended from the lower rim of the entrance. Fig. A2 shows the form of selected nests. Nests a, b, d and e were truly pensile, while c, from the crown of a kanuka, was securely stayed by the beard. Nests f, g and h had many lateral attachments and were built in thickets of leaves and twigs. Plate 4 illustrates other nests.

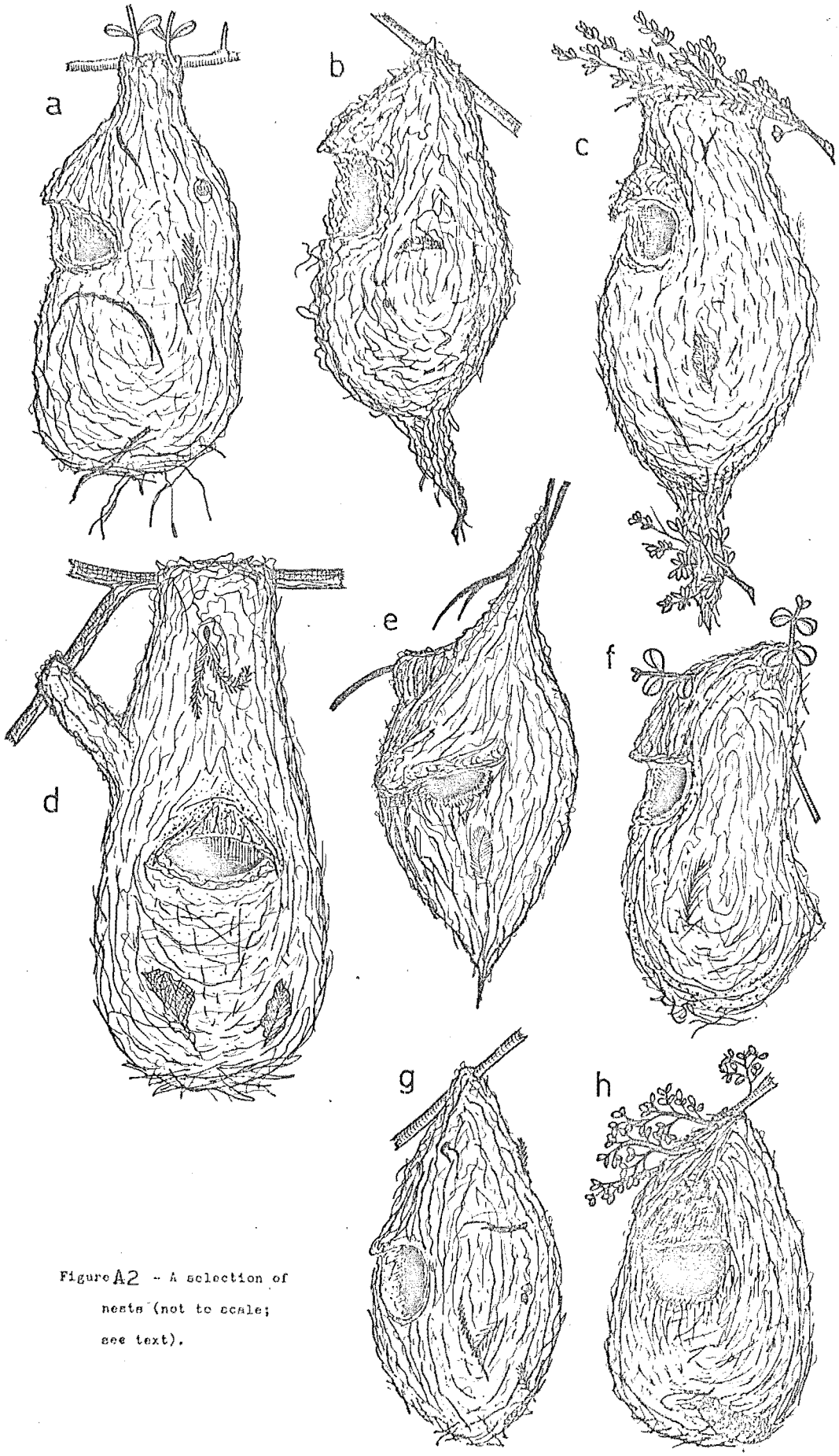


Figure A2 - A selection of nests (not to scale; see text).

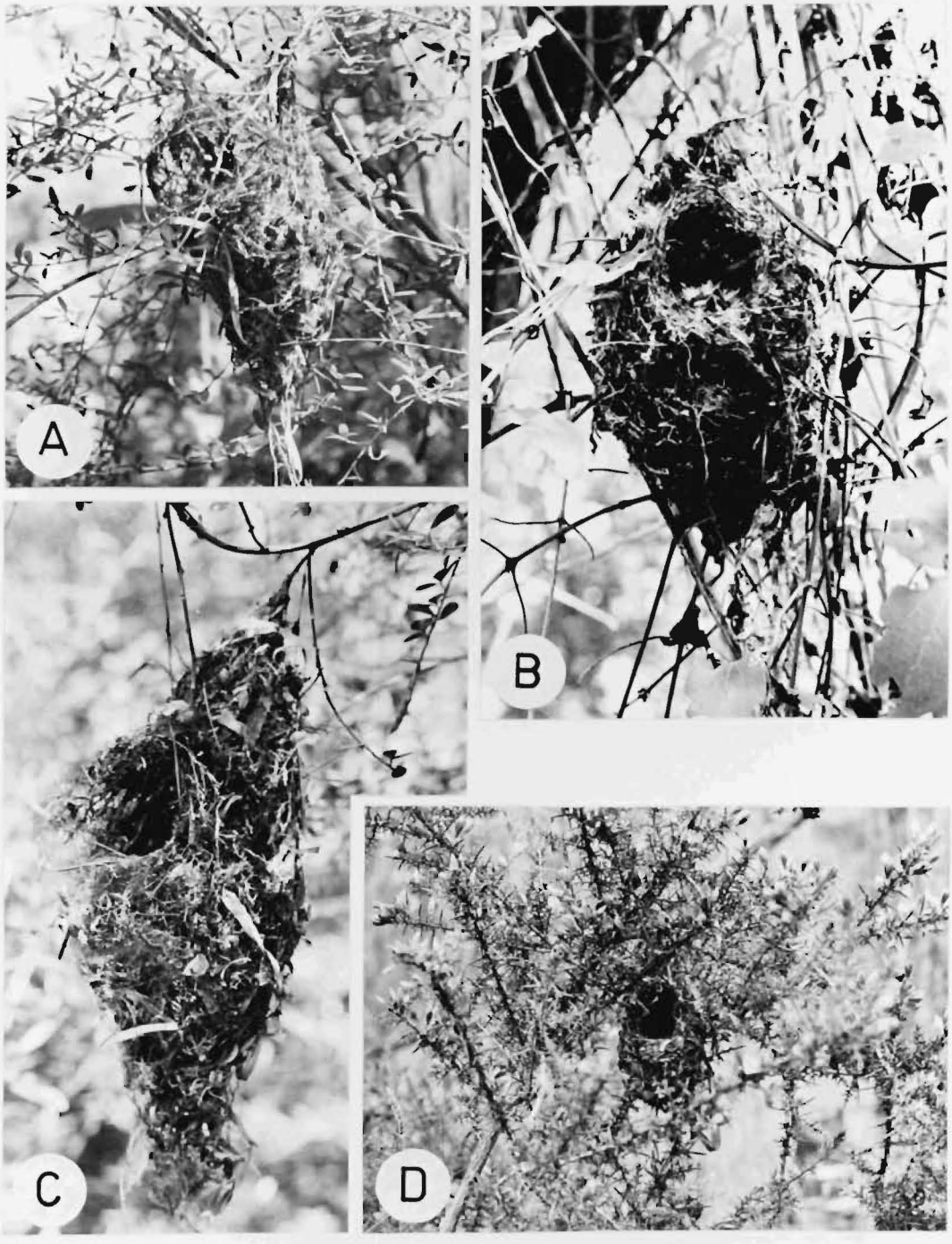


Plate 4 - Nests. (A) Pensile nest with prominent hood (in *Coprosma propinqua*; 2 m above ground). (B) Semi-pensile nest (*Clematis vitalba*; 3.5 m) containing four nestling warblers (8-9 days old; two visible at entrance). (C) Precariously attached pensile nest (*Cytisus monspessulanus*; 1.5 m). (D) Pensile nest without beard (*Ulex europaeus*; 1 m).

APPENDIX 3 - Morphological development of nestling warblers.

THE NEWLY-HATCHED WARBLER AND ITS NATAL PTERYLOGRAPHY

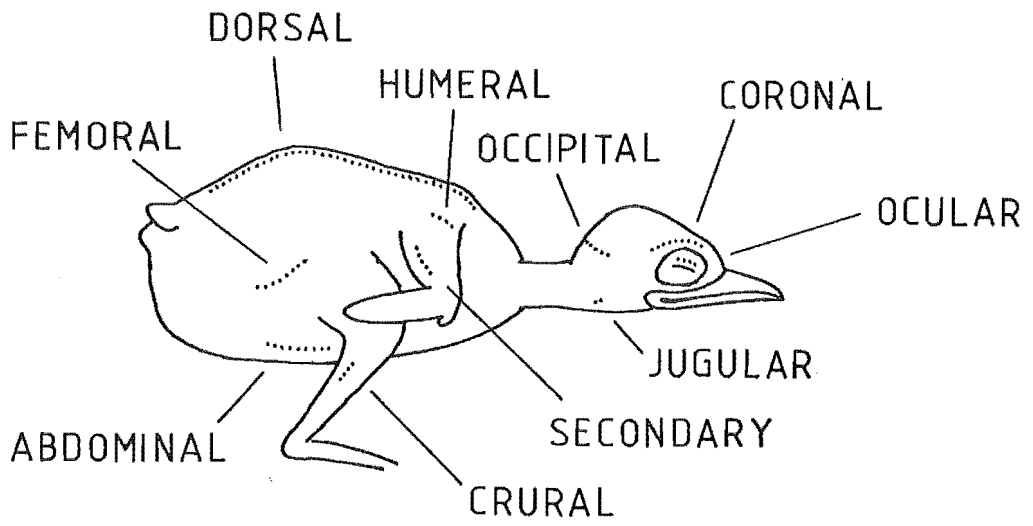
Two warblers at hatching weighed 0.8 g and 1.15 g, and of 83 nestlings weighed within 24 hours of hatching 14 were 1.0 g and a further seven were 0.85-0.95 g, these presumably having recently hatched. Thus the weight of newly-hatched warblers was about 1 g, often a little less.

The newly-hatched nestling (Plate 5B) had pink or greyish skin, slightly darkened dorsally where pterylae later formed. Dorsal surfaces sported dense, white natal down, and rictal flanges were white. The bill was grey except for a black tip, and the claws were dark grey. There were bristles less than 1 mm long on the caudal tract and primary and secondary alar tracts. Newly-hatched nestlings rested on their abdomen in the foetal or "egg" position characteristic of most altricial birds (Banks 1959).

Nestlings were dimorphic in skin-colour, 32% of those examined (n = 87) having distinctly grey skin, and the rest being pink. The morphs occurred singly or together in broods, and while in most cases nestlings were clearly assignable to one or other category, continuous variation was suggested by others. The significance of the dimorphism is obscure, and its manifestation was later hidden by plumage, which was identical in both types.

Many species of birds hatch with a natal down of neossoptiles which are pushed from their follicles by the ensheathed teleoptiles ("pin-feathers") that develop subsequently, and to which the down remains attached until the juvenile feathers unfold (Pettingill 1970). The distribution of natal down in newly-hatched passerines varies (Boulton 1927, cited by Saunders 1956), and it is absent in some species. Otherwise it occurs mainly on dorsal surfaces (Saunders 1956) in shades of white, grey, brown or black. The tufts and rows of neossoptiles match the arrangement of pterylae only generally, and separate naming and discussion of each is necessary. I followed Saunders' (1956) nomenclature of down-patches of passerines (Fig. A3). Occipital and dorsal patches are median; the others paired.

Most of the grey warbler's down was on the head and back. Of the 12 down-patches described by Saunders, three (the primary, caudal and lateral patches) were absent in the grey warbler. However, there was an additional ventral paired patch near the throat, which I called the jugular. Nearly 80% of nestlings (n = 45) had single or multiple tufts of jugular down to one or both sides of the throat. The ocular patch



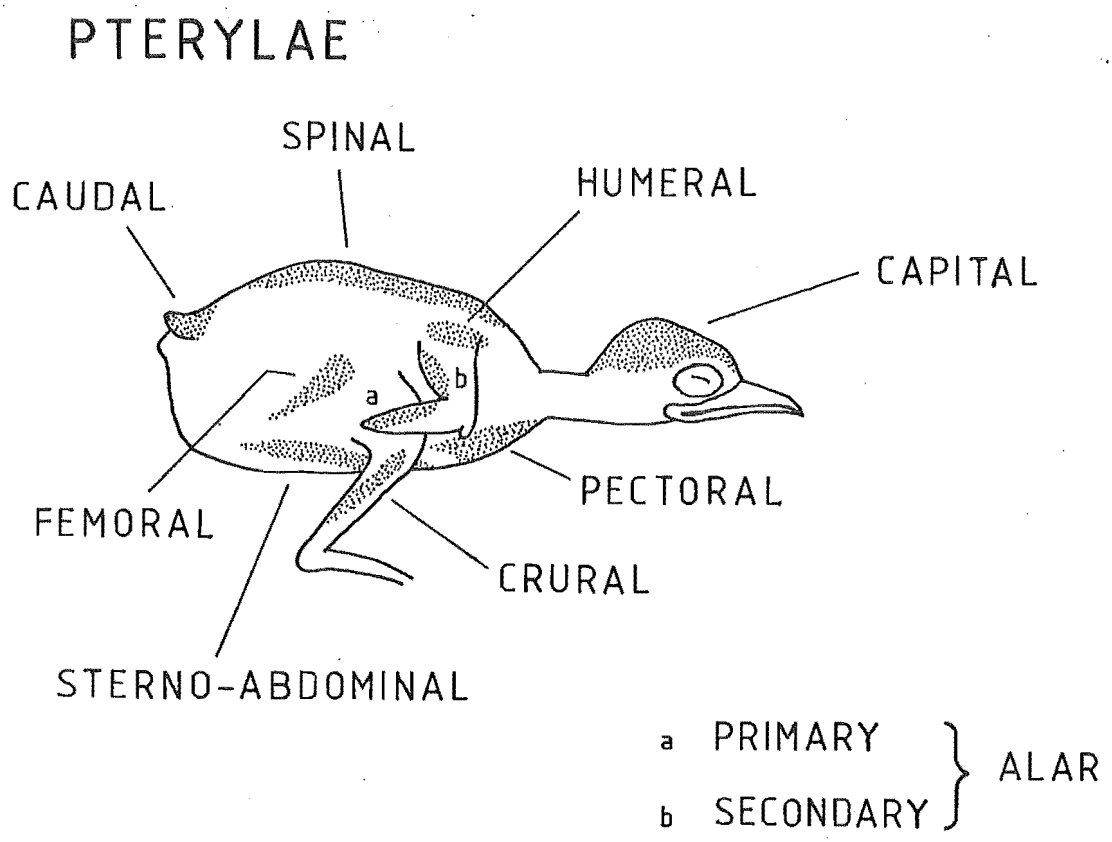


Figure A 3 - Nomenclature of the down-patches and pterylae of grey warblers (after Saunders 1956 and Lucas & Stettenheim 1972, respectively).

(on the eyelids; Plate 5A) present in the warbler, was seen only in a tyrannid flycatcher by Saunders, who predicted erroneously that it would not be found in song-birds. Three-quarters of the warbler-nestlings had a dorsal patch in two sections separated by a gap, but in some it was continuous and in others nearly absent. Crural down was rare, 10% of nestlings having a minute tuft on one or both thighs. Crural and jugular down was insignificant, variable in occurrence, and probably vestigial; I completely overlooked it during the first breeding-season.

The neossoptiles (as seen in full-term embryos from unhatched eggs; Plate 5A) were in rows rather than patches, many at the ends of rows being shorter than the rest. Neossoptiles of the ocular, coronal and abdominal patches were in a single row, while those of the occipital, secondary, humeral and femoral patches were in a double row, though not always paired. Neossoptiles were paired in the anterior part of the dorsal patch, but formed a single row posteriorly, highly suggestive that two separate patches were involved.

PHYSICAL DEVELOPMENT

I described the external development of grey warblers from regular examination in the field of 40-60 nestlings in total. The developmental sequence was uniform, but the rate varied between individuals, and what follows is a composite description of the kind given by other authors (eg. Banks 1959, Anderson and Anderson 1961) under similar circumstances. Nestlings on day 0 (the day of hatching) are described above.

The nomenclature of major pterylae (Fig. A 3) follows Lucas and Stettenheim (1972: 74-5).

Day 1-2 The skin changed to a deeper grey on all dorsal surfaces and on the legs. Skin covering the eyes slit in many cases, and the rictal flanges turned pale yellow or remained white.

Day 3-4 Emerging pin-feathers (ensheathed teleoptiles) were visible along the pectoral and sterno-abdominal tracts, and on the alar tracts they were up to 2 mm long (including the terminal bristle which was visible at hatching). Skin over the eyes slightly parted in some cases. Rictal flanges were mostly yellow or bright yellow (with buccal skin and tongue to match); only a few remained white.

Day 5-6 Pin-feathers of the capital, caudal, femoral, humeral and crural tracts were less than 1 mm long; those of the spinal, pectoral and sterno-abdominal tracts reached 1 mm; primary pin-feathers were up

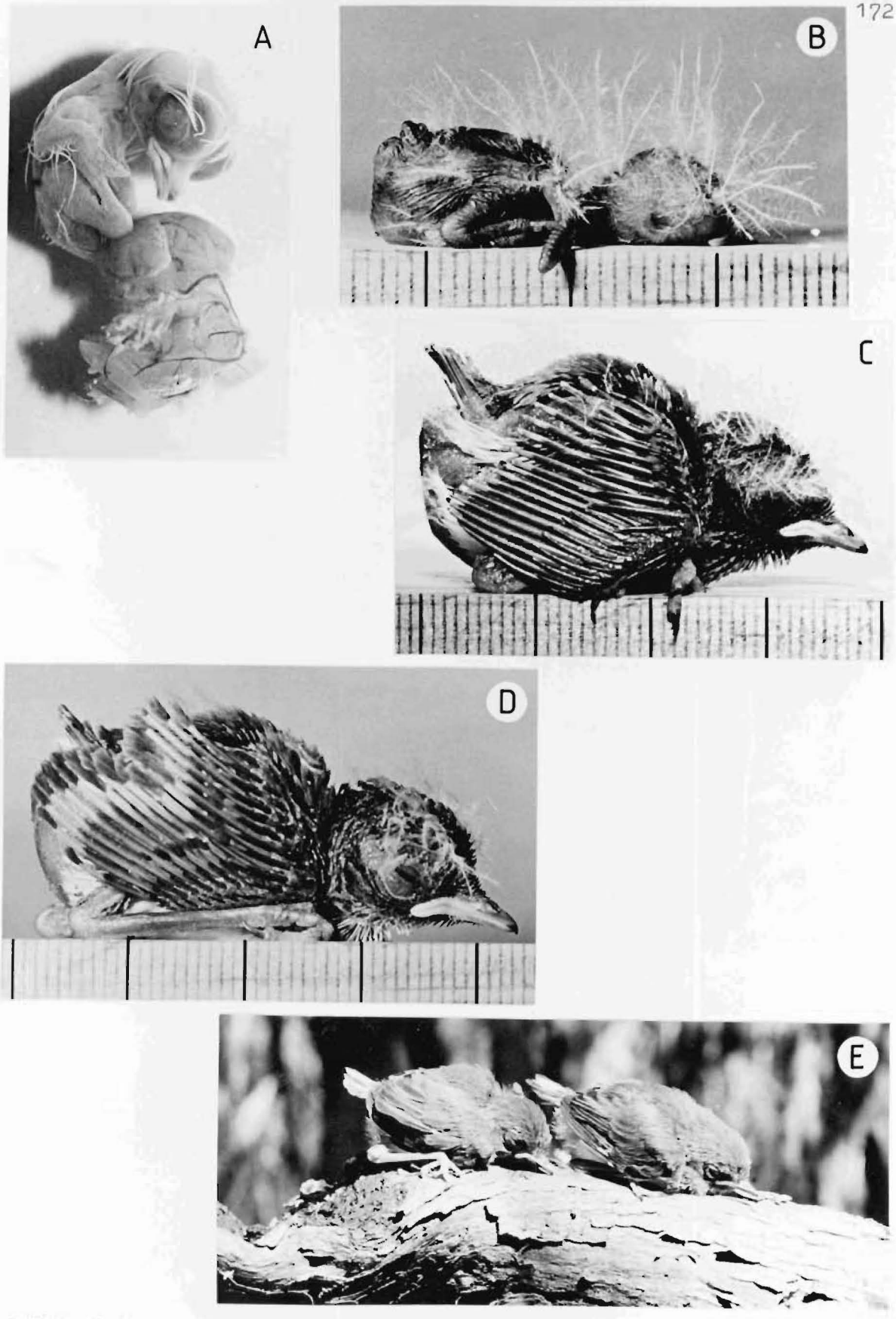


Plate 5 - Developmental stages of the grey warbler (scales in mm). (A) Full-term embryo (under water) showing yolk-sac and natal down. (B) Nestling on day of hatching. (C) Nestling c.8 days old. (D) Nestling 12 days old. (E) Nestlings 15 days old.

to 5 mm; and those of the secondary tract extended to 4 mm. The opaque sheaths showed the colour of the underlying teleoptiles, which were grey except in the sterno-abdominal and femoral pterylae where the pale breast and flank feathers developed. All rictal flanges were yellow (cream-coloured to bright yellow).

Day 7-8 (Plate 5 C.) Feathers of the spinal, pectoral, sterno-abdominal and femoral tracts were first to emerge from their sheaths. In some individuals the primary and secondary remiges, and feathers of the capital, humeral and crural tracts also erupted. Feathers of the sterno-abdominal and femoral pterylae were white, the others grey. Rectrices remained ensheathed. The longest primary pin-feather extended to 10-12 mm before the sheath disintegrated; the longest secondary pin-feather was a little shorter. Spinal, pectoral, sterno-abdominal, femoral and humeral pin-feathers did not exceed about 3 mm, and capital and crural pin-feathers reached a maximum of 1.5 mm. Some nestlings lost the egg-tooth (but see Plate 5C); most had half-open eyes. Legs were dark grey-pink except for conspicuously pale skin about the ankle.

Day 9-10 Feathers of the caudal tract erupted before the intact sheaths exceeded about 4 mm. Most feathers in all pterylae were at least partly un-sheathed, but much natal down persisted, presumably at the tips of intact pin-feathers.

Day 11-12 (Plate 5D.) White keratinous flakes were shed in large quantities from disintegration of the sheaths, especially those of the remiges. The remiges extended to 20 mm from base to tip, while the longest rectrix was barely 10 mm. The bill darkened from tip to base and the legs became greyer. Many nestlings had yellowish ankles and a pale stripe along the posterior edge of each tarsometatarsus. Some nestlings still retained the egg-tooth.

Day 13-17+ No sheaths or apteria were externally visible on nestlings resting with their wings folded (Plate 5E). The ventral apterium and much of the nakedness under the wing was occluded at fledging. The longest remex approached 30 mm, while the longest rectrix was 15 mm. The tail was short at fledging as in most song-birds. Natal down sometimes persisted on the head even at fledging. Small yellow feathers developed in the orbital region. At fledging the claws were black, the legs distinctly grey with paler soles, and the bill dark grey with a black tip. Eyes opened fully revealing dark brown irides.

APPENDIX 4 - Morphological development of nestling cuckoos.

THE NEWLY-HATCHED CUCKOO

One cuckoo at hatching weighed 1.2 g, and six nestlings within 24 hours of hatching weighed 1.2-1.7 g. Therefore newly-hatched cuckoos were only slightly heavier than newly-hatched warblers (about 1 g; Appendix 3), despite the four-fold difference in the weight of adults.

The newly-hatched cuckoo (Plate 7A) had dark grey skin, apart from a dorsal pink area at the base of the neck which sometimes extended onto the back and belly. The head and back were sparsely covered in coarse, white, hair-like natal down (trichoptiles), and rictal flanges were white. At its base the bill was pink, otherwise grey, and the mouth and tongue were pink. The legs were grey with pale soles and white claws, and there were bristles less than 1 mm long on the caudal and alar tracts. Nestlings rested in the foetal position, and unlike newly-hatched warblers, were able to grip with the toes and cheep. The toes were facultatively zygodactylous.

Newly-hatched cuckoos were easily distinguished from warblers by the former's large external nares (with raised rims), fleshy alular lobes, zygodactylous toes, and non-fluffy natal down. However, the young nestlings of both species were similar in size and in the colour of skin, natal down, rictal flanges, bill and legs. Nestling brown creepers, closely related to the warbler, had orange skin, yellow rictal flanges and fawn natal down. It is hard to imagine why nestling cuckoos and warblers, in separate orders, should have so strong a resemblance unless selection has favoured mimicry of the host by the parasite.

It has been supposed (eg. Payne 1977) that young brood-parasites which evict eggs or nestlings do not closely resemble the host's young, and mimicry is only known where the parasite and host's young are raised together (Lack 1968). Shining cuckoos nearly always co-existed with warblers for a few days initially (section 11.2), and mimicry may thus be valuable. The implication that warblers would reject a strange nestling, is puzzling when the female accepts a strange egg. However, while only the female warbler attends to eggs, and may rely on tactile rather than visual stimuli, both sexes feed the nestlings and intimate visual contact may be important.

The young of cuckoos (Cuculidae) were long supposed to be naked at hatching until bristle-like natal plumage was discovered in nestlings belonging to several cuculid sub-families (eg. Coccyzinae, Centropodinae;

Miller 1924). Shelford (1900) described hair-like natal feathers up to 4 cm long in *Centropus sinensis*, and termed them "trichoptiles". All evidence, however, has indicated nakedness in the newly-hatched young of the Cuculinae. Miller (1924) reported that nestlings of *Cuculus* and *Chrysococcyx* lack natal down, and this was confirmed for the African glossy cuckoos (Jensen and Jensen 1969, Jensen and Vernon 1970). Naked nestlings of *Cuculus canorus* and *Chrysococcyx klaas* are illustrated in Wyllie (1975; plate 48) and in Jensen and Clinning (1974; figure 13A) respectively. Nestlings of *Ch. basalis* and *Ch. lucidus plagosus* are naked at hatching (McGilp 1941, Courtney and Marchant 1971). Thus shining cuckoos are exceptional in possessing natal down.

The natal down of shining cuckoos (Plate 7A-C) is restricted to coronal, occipital and dorso-lateral patches. The positions of the first two are as shown in Fig. A3. Whereas passerines have a median dorsal patch of down, the shining cuckoo has two dorso-lateral patches corresponding with the bilaterally paired spinal pterylae. In the cuckoo each neossoptile is a filamentous trichoptile, whereas in warblers the neossoptiles are branched and fluffy (Fig. A 4). There are about 40 long trichoptiles on the head (particularly in the coronal patch) and about 16 on the back. In addition there are many shorter thinner ones on both back and head. In some cuckoos a row of minute bristles suggested a vestigial ocular patch.

PHYSICAL DEVELOPMENT

The introductory remarks on the development of warblers (Appendix 3) apply here, except that the total sample of nestling cuckoos was 16. Stages of development (I recognised four) were more variable in duration than for warblers because the nestling period of cuckoos was longer and apparently more plastic. The extent to which cuckoos of the same age varied in their stage of development is shown by Plates 6C and 7D-E. A major difference in pterylosis between the shining cuckoo and grey warbler is that the cuckoo has a pair of spinal pterylae, united posteriorly but otherwise separated by a median dorsal apterium. Excepting this, the names and positions of pterylae in the cuckoo are as shown in Fig. A 3.

Day 1-5 (Plate 7B.) The skin darkened to deep grey or black, especially dorsally, and the claws turned grey. The bill darkened, especially dorsally and terminally, and the tongue developed a grey tip. Eyes partially opened (revealing dark brown irides) and rictal flanges changed to pale yellow in most cases.

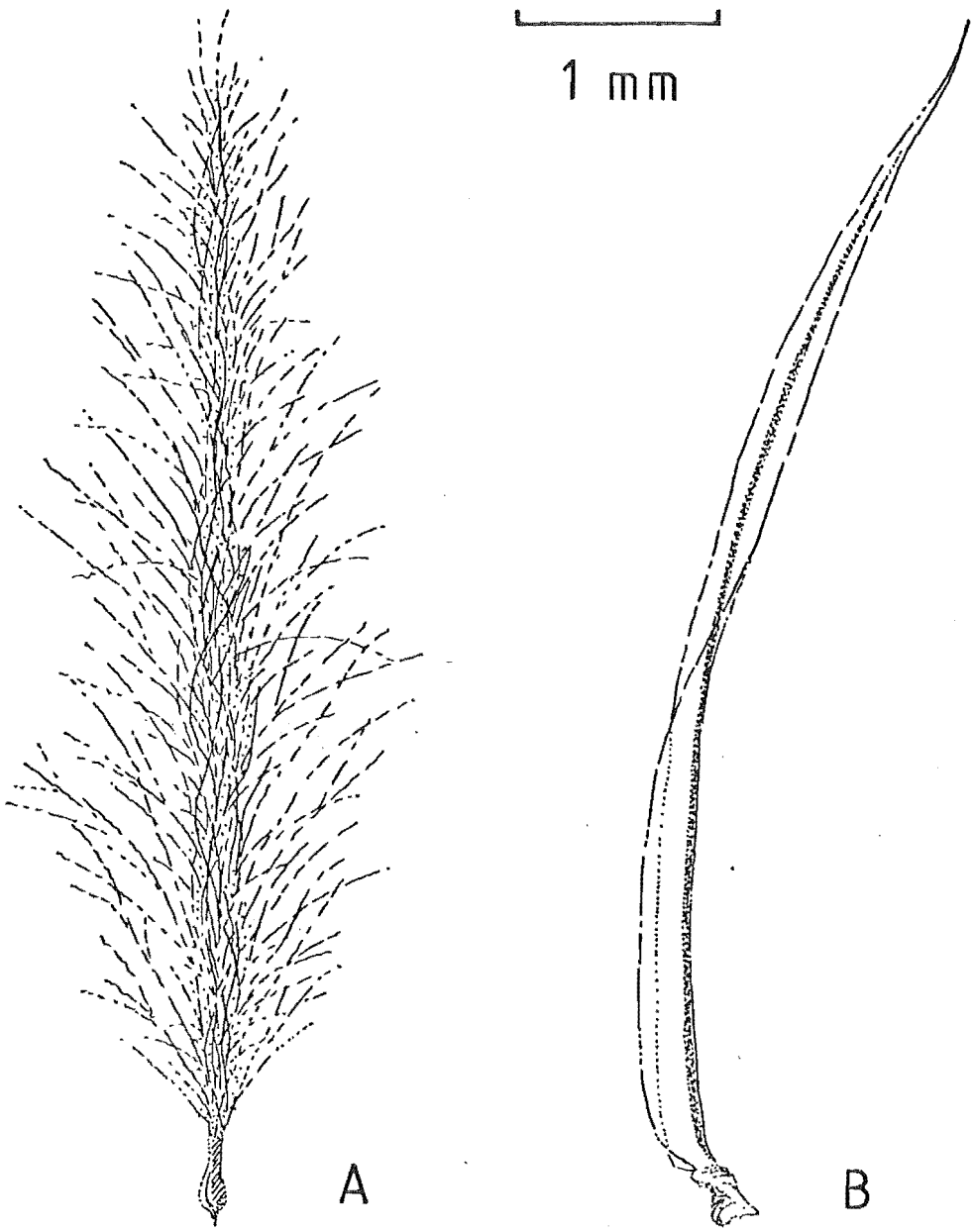


Figure A4 - Natal feathers. (A) Neossoptile from a nestling warbler. (B) Trichoptile from a nestling cuckoo.

A

B

C

D

Plate 6 - Developmental stages of the shining cuckoo (I). (A) The egg (right) beside the host's (left) from the same nest (scale in mm). (B) Nestling 10 days old. (C) Nestling 15 days old. (D) Nestling c.19 days old, just before fledging.

Plate 7 - Developmental stages of the shining cuckoo (II; scales in mm). (A) Nestling at hatching. (B) Nestling 1 day old. (C) Nestling 6 days old. (D) Nestling c.14 days old. (E) Nestling c.15 days old in defensive display. (F) Nestling c.19 days old.

Day 6-9 (Plate 7C.) The skin became dull orange where ventral pterylae were forming. Pin-feathers (or at least the bristles terminal to them) were visible on all tracts, and reached up to about 7 mm on the alar. Pin-feathers of the pectoral and crural pterylae were bright orange-yellow, and all others were dark grey or black, except those of the sterno-abdominal and femoral pterylae which were mixed. By day 9 at the earliest, the tips of many pin-feathers had admitted air and turned pale. The legs became blue-grey with pale yellow soles. Eyes fully opened.

Day 10-14 (Plates 6B, 7D.) Humeral and alar feathers were often first to erupt from their sheaths, on day 10 at the earliest. By day 14 most feathers were erupting in all pterylae and nearly all natal down was shed. Dorsal plumage was an iridescent brownish-green, while feathers of the breast and belly were yellowish. Most of the bill was dark grey, and rictal flanges, which did not change beyond pale yellow, were regressing. The edges of the buccal lining were sometimes yellowish.

Day 15-19+ (Plates 6C-D, 7E-F.) The first iridescent green bar on the otherwise yellow ventral feathers was visible from about day 15. Sheaths became less conspicuous externally as the plumage developed, and the ventral apterium was occluded before fledging. As with most altricial birds, rectrices did not fully develop in the nestling. The egg-tooth was shed at about 15-17 days, and the bill began to turn black.

Developmental stages of the shining cuckoo are similar to those described for *Chrysococcyx klaas* (Jensen and Clinning 1974, fig. 13) and *Ch. caprius* (Jensen and Vernon 1970). Apart from lacking natal down, nestlings of the latter appear to differ from *lucidus* only in minor details such as coloration.